Effects of Megafaunal/Macrofaunal Burrowing Interactions on Benthic Community Structure

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A Thesis submitted for the degree of Doctor of Philosophy

to the Faculty of Science at the

University of Glasgow

April 1988

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ACKNOWLEDGEMENTS

I would like most of all to thank my supervisors Dr R.J.A. Atkinson and Dr T.H. Pearson for their guidance, support and constructive criticisms.

This research was carried out under the tenure of a CASE Award from the Natural Environment Research Council to the University Marine Biological Station Millport (University of Glasgow) and the Dunstaffnage Marine Research Laboratory of the Scottish Marine Biological Association. I gratefully acknowledge the facilities provided by the directors of both establishments, Professor J.A. Allen (Millport) and Professors R.I. Currie and J.B.L. Matthews (SMBA).

Many days were spent at sea on the boats from both Millport and Oban and I thank the skippers and crews of R.V. "Aora", R.V. "Aplysia", R.V. "Calanus", in particular Mr I. Drummond on R.V. "Seol Mara", for their interest and help. Similarly I would like to thank the Chief Divers, Mr A.V. Gale (SMBA), and Mr P. Lonsdale (Millport) for their support. Both they and the diving teams of both establishments (S. Anderson, K. Cameron, C. Comely, D. Donan, G. Duncan, M. James and others), put up with uncomfortable conditions, cold murky waters and adhesive resin.

Gordon Duncan was invaluable for his practical help and he overcame many obstacles, always with a smile.

I would like to acknowledge the help of DAFS, Aberdeen for allowing access to information on the Garroch Head dumping ground.

During the production of this thesis Dr C.G. Moore and Miss A. Duff provided computational help with some of the statistical problems, Mrs C. Lafferty skilfully produced the photography and Mrs M. Fletcher typed for many long hours on the final copy.

This thesis had much in common with the gestation period of an elephant but the labour was far more extensive. Family, friends and colleagues held my hand and soothed my brow. To them, thank you.

ABSTRACT

Megafaunal burrowing organisms are, in comparison to the macrofauna, mostly sparsely distributed, inhabiting deep sedimentary levels below regular sampling depth. They have been little studied until recent advances in sampling methodology. As large scale bioturbators, they have a high potential impact on the sedimentary environment and its inhabitants. This thesis assesses both the role of megafaunal burrowers in controlling macrofaunal community structure, and some of the mechanisms involved. Megafaunal burrowers are also subject to controlling forces which may directly or indirectly affect the macrofaunal community. Two of these factors, organic enrichment and fishing pressure were investigated.

Four "typical" west coast of Scotland sub-littoral inshore soft sedimentary sites were surveyed: Loch Creran, under the influence of an organic effluent from an alginate factory; Loch Riddon, under the influence of general eutrophication; Camas Nathais, under fishing pressure for the megafaunal burrower Nephrops norvegicus, and Creag Isle, taken as a relatively undisturbed "control" site. Megafaunal, macrofaunal and sedimentary characteristics were analysed. Organic enrichment was responsible for high numbers of relatively immobile surface feeding macrofaunal species at the two former sites. The control site had the highest megafaunal abundance with an increase in the sediment/water interface of 27%, from the internal surface area of large burrows. The predominant non-stochastic factors that seem to determine megafaunal community structure are a complex interaction of sedimentary characteristics, organic carbon content and, to a lesser extent, depth. These factors, especially organic carbon content, were also important in regulating macrofaunal community structure. Megafaunal burrowers were further responsible for localized structuring.

The localized effect of burrower/burrow presence was investigated on a fine scale in the field by diver coring around the burrow of Nephrops norvegicus and in an adjacent unburrowed area. The burrowed area had a more homogeneous sedimentary fabric with sedimentary depth, indicative of vertical mixing. Redox potentials and organic carbon content showed greater variability with sedimentary depth. Macrofaunal abundance and biomass were lower in this area and this was reflected by the low numbers of surface feeding, discretely motile and tubiculous polychaetes.

In the experimental aquaria, mesocosm tanks were used to substantiate the field observations and to further investigate the mechanisms of megafaunal effects. Different burrowers were found to cause both detrimental and enhancing effects which were dependent on their activity and life mode. Nephrops norvegicus, a large surface-active burrower, had a more inhibitive effect. It excluded surface feeding species by increased turbidity and burial, and generally inhibited macrofaunal activity. However, lack of competition and continual perturbation allowed colonization around the burrowed area by a small opportunist population of nematodes and oligochaetes. Calocaris macandreae, a less active burrower that remains sub-surface, had a less marked detrimental effect on macrofaunal community structure. It is suggested that this burrower attracted a number of species by providing organic rich excavated sediment (for example, Corbula gibba, Turritella communis, Magelona filiformis and Paraonis gracilis.

Megafaunal abundance was investigated by remote video along an organic gradient at the Garroch Head sludge dumping ground in the Clyde. Abundance decreased with increasing organic content of the sediment in towards the centre of the ground. It is suggested that the major causes were due to sedimentary modification from increased fine material, effects on juvenile forms and general anaerobic sedimentary conditions. The response of different species varied and was related to their tolerance to the above-

mentioned factors. The implication of megafaunal absence is discussed in relation to macrofaunal community structure and it is suggested that macrofaunal changes along an organic enriched gradient may be more abrupt than expected at the point where megafaunal species are excluded.

The role of biological interactions in determining macrofaunal community structure is reviewed. Megafaunal interactions, which include aspects of competition, predation, disturbance and enhancement, are discussed with respect to the established theories. It is suggested that megafaunal burrowing organisms have an important role in increasing spatio-temporal heterogeneity in temperate marine soft sedimentary communities.

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CHAPTER 1. INTRODUCTION

Most of the sea-bed is of a sedimentary nature, ranging from deep abyssal red clays to coarse grained oceanic beaches. The greater proportion, however, are fine grained deposits of clay or silt-sized particles and are located predominantly on the continental slope, rise and abyssal plane. The emphasis of historical study has, however, been focussed on the shore, in particular on rocky substrata, due mostly to the ease of observation. An understanding of the biology of sedimentary substrata was, in the past, difficult as the fauna usually lay buried and had to be sampled "blind" and destructively (Gray, 1981).

During the early part of this century, pioneer quantitative studies of the soft sedimentary marine benthos were made by C.G.J. Petersen (1913). He sampled the macrofauna of the shallow waters off the Danish coast, recording the species present, their abundance and biomass. Benthic communities were designated by the identification of characterizing species. Characterizing species were those that were non-seasonal with long life-spans and were numerical or biomass dominants, typical of a given assemblage (i.e. temporally and spatially persistent). These criteria were later used to define "equilibrium" species (McCall, 1977). Thorson (1957) extended and popularized these ideas. He noted similar genera in communities that were widely separated and therefore classified these communities in terms of their most obvious genus rather than species (which varied with differences in local conditions). He called these assemblages parallel communities.

It became apparent from the 1960s onwards that communities could not be adequately described by the rigid definitions of Petersen and Thorson. Species are distributed along a continua, each with its own unique niche, and boundaries between communities are usually indefinite with intergrading along transitional zones. Wherever the environment changes with locality, there

are corresponding adjustments in the make-up of the assemblage of species. The Petersen-Thorson type characterization of communities, however, still holds as useful summarizing descriptions, if rigidity is not implied.

Some effort was made in the past to relate communities to their localized physical and chemical environment, in particular, to the sediment type occupied (Petersen, 1913; Jones, 1950; Thorson, 1957; Glemarec, 1973). For example, Petersen's (1913) Echinocardium-filiformis community (characterized principally by the heart urchin Echinocardium cordatum and the brittle star Amphiura filiformis) occurred in sandy mud, whilst his Brissopsis-chiajei community (characterized by the heart urchin Brissopsis lyrifera and the brittle star A. chiajei) occurred in soft, silty mud. Other physical factors that have been used to subdivide these types of community include salinity, temperature, depth and water movement.

A close relationship has been demonstrated between species present and sediment type, in particular through larval settlement. Wilson (1952) for example, showed that preference for a particular grain size stimulated metamorphosis and settlement in the larvae of the polychaete Ophelia bicornis. Gray (1974) has reviewed some of the processes involved with larval settlement and substrata selection. The factors are understood to be complex and involve response to the structure and contours of the surface (less important in sediment dwelling organisms), grain size characteristics (including pore size and porosity), inorganic and organic compounds, presence of microbial films, presence of populations of the same species and other factors (which may include specific reproductive strategies such as brooding or direct development). Thus biological factors are just as important as the localized physical and chemical environment of a sediment for providing settlement stimuli.

The possibility that biological interactions could generally influence a marine benthic community structure has only relatively recently been a point of study and discussion. Tevesz & McCall (1983) stated:

> "A major theme running through benthic ecological literature from the late 1800s to the present is the relative importance of physical environmental factors such as temperature, salinity, and substratum type versus biological factors such as competition, predation, amensalism, disease and parasitism. We think it is safe to say that until fairly recently, most workers with few exceptions subscribed to the notion that biologic interactions had little effect on distribution and abundance."

Tevesz & McCall considered the reasons for this to be as follows:

> "The dominance of this view may be ascribed in large measures to the way bottom communities were studied: from the deck of a boat, with a grab sampler and large-mesh sieve that did not collect early life stages, and over an area of many square miles. In situ observations and small scale observations were difficult to make."

The development of direct observational techniques [by the use of photography and television (see Holme, 1984), SCUBA diving (see Gamble, 1984) and the use of experimental aquaria]; accurate small scale repeat sampling techniques [with the help of modern position fixing methods (see Holme & Willerton, 1984) and in situ methodology]; and the use of manipulative experiments in the field and experimental aquaria, has lead to a wealth of information on such soft-sedimentary biological interactions as: competition, predation, amensalisms, disturbance and adult-larval interactions. A more detailed review of these complex, inter-related interactions and their possible role in the determination of benthic community structure is given in the final discussion of this thesis.

The effects of biological interactions can be broken down into direct effects between organisms and indirect effects mediated through change in the physico-chemical properties of the sediment.

Direct effects are nearly always inhibitive and are due to either predation or competition. Predation can be either sub-lethal or lethal. Many visual epifaunal predators have sub-lethal effects, for example, the flatfish,

plaice and dab feeding on polychaete tentacles and tails (de Groot, 1971; de Vlas, 1979). Sub-lethal encounters have also been reported infaunally by Witte & DeWilde (1979), where a nereid polychaete was observed to feed on the tail of an arenicolid polychaete. Lethal encounters occur at several trophic levels in sedimentary environments (Ambrose, 1984a) with epifaunal predators feeding on infaunal predators which are feeding on infaunal prey. Epifaunal predators as diverse as rays (VanBlaricom, 1982), shrimps (Pihl & Rosenberg, 1984) or whales (Oliver et al., 1984) feed selectively or non-selectively on a wide variety of near-surface dwelling benthic organisms. Within sediments, Commito & Ambrose (1985a, 1985b) and Commito & Shrader (1985) have reported on the existence of several trophic levels, consisting predominately of predatory polychaetes (for example, phyllodocid, nereid and nephtyid polychaetes).

Direct competition in terms of interference may have a similar effect to predation in that it may ultimately be lethal, unless the victimized organisms possess tolerance or avoidance mechanisms. Levin (1982) observed strong aggression behaviour between different species of spionid polychaetes, which resulted in the emigration of a competitively inferior species. Displacement may also be termed an interference mechanism, but is perhaps less direct. It is not necessarily mediated through a change in physical or chemical properties, but more through bulk sediment movement. Epifaunal pit diggers (for example, the crab Cancer pagurus -Thrush, 1986) or large scale burrowers and sediment bulldozers may exhume, push aside or further bury infaunal organisms.

Infaunal organisms must by their lifestyles affect the environment they live in. Any environmental changes brought about by their activity will then have a strong possibility of affecting another organism or suite of organisms. These indirect interactions may be either inhibitive or enhancing with respect to other organisms. Rhoads & Boyer (1982) noted that physical sedimentary

modifications were highly correlated with certain aspects of benthic organisms, in particular: method of feeding, feeding selectivity, feeding level in the sediment, degree of mobility, size, density, burrowing depth and if the organisms were tube dwelling, density, spacing and length of the tubes. These factors govern the site, rate and extent of bioturbatory activity of the benthos. Indirect biological interactions can be mediated through a number of different sedimentary factors and processes affected by bioturbatory activity, involving: change in grain size, sedimentation/resuspension and transfer of water, particles and solutes, with associated effects on chemical processes. These types of animal-sediment relations have been recently reviewed in McCall & Tevesz (1982).

Organisms feeding on suspended or deposited particulate matter will elicit a change in grain size distribution, grain shapes and spatial segregation of grain sizes (Rhoads, 1974). Suspension feeders remove materials from suspension and incorporate them into the sediment in aggregated faecal pellets, the size and shape of which can be species dependent (Moore, 1931b). Deposit feeders aggregate particles into faecal pellets from different levels in the sediment. Pellets commonly make up large proportions of surface sediments, 30-50% in the Clyde Sea area (Moore, 1931a). If deposit feeders feed selectively on a particular size of particle, at a particular horizon in the sediment, it may result in a biogenic graded bedding (Aller, 1982). Rhoads (1974) reported that a number of vertically orientated deep deposit feeding polychaetes and holothurians, feed only on specific sizes of fine grained particles, transporting them vertically to be defaecated as aggregates, leaving a residium of large particles at depth. As noted above, larvae of some organisms select for a particular grain size and so may be excluded from areas of changing modal grain size. The surface deposit feeding gastropod Hydrobia minuta has been shown to stop feeding when surface sediments become completely pelletized, only resuming feeding when pellets have started to

break down (Levinton et al., 1977). It was suggested that the pellets were low in organic content after digestion and that feeding resumed when the pellets were colonized microbially, after they had started to break down, boosting their organic content.

Porosity and water content are dependent on grain size distribution. Porosity is a measure of the interstitial pore space, the surface area of which is an important site for microbial colonization and enhanced production (Webb, 1969). Pellet formation increases pore size through loose packing. High porosity would probably increase the diffusive permeability of a sediment, lowering the redox discontinuity layer and increasing the living space available for infaunal organisms.

The ease with which free-living infaunal burrowers move through and feed upon sediments, is known to be a function of sediment water content and state of compaction (Chapman, 1949). Bioturbation increases sediment water content (Rhoads & Young, 1970). Rhoads & Boyer (1982) noted that areas of intensive particle bioturbation, characteristic of equilibrium communities generally had water contents of 60-70%, facilitating a burrowing mode of life. This was in contrast to early successional communities, with low orders of bioturbatory activity, which exhibited less than 60% water content and a greater amount of compaction.

By increasing water content and breaking up the sedimentary fabric, bioturbation decreases bottom stability and promotes erosion by facilitating resuspension. This may deter sessile suspension feeders which can be inhibited by the clogging of filtering structures, the resuspension and burial of their newly settled larvae and the general discouragement of their larvae from settling (Rhoads & Young referred to this phenomenon as "trophic group amensalism"). In contrast, biodepositing suspension feeders can increase the stability of sediments. High densities of elements that cause increased bed roughness (including dense stands of tubiculous organisms), may increase

sedimentation from altered bottom current regimes (see Rhoads & Boyer, 1982). Individual tubes of sessile organisms can, however, enhance bottom erosion, resulting in eventual washout of the whole population (Ekman et al., 1981).

Some stabilizing mechanisms are less obvious, such as the interactions between macrofauna, meiofauna and microfauna. As stated above, bioturbation may increase interstitial pore size and enhance microbial production. Microbial mucopolysaccharide exudates may then bind particles together. Macrofaunal and meiofaunal organisms also produce mucous secretions with adhesive properties, for example, nematodes can produce binding mucous secretions which can in turn stimulate microbial metabolism (Heip et al., 1982).

Irrigation associated with bioturbation is of considerable importance in controlling biochemical and chemical sedimentary processes. Aller (1982) has recently reviewed the effects of the macrobenthos on these processes. He noted that most reactions were associated with decomposition of organic matter and other biogenic compounds. These reactions influence pH and redox potential, causing depletion and build-up of characteristic reactants or products. In a homogeneous sediment devoid of meiofaunal and macrofaunal organisms, decomposition reactions would, in principle, be vertically stratified below the sediment-water interface. Aller suggested that the macrobenthos influenced this hypothetical reaction distribution in four major ways: "1) material is translocated continuously between reaction zones during feeding, burrowing and tube construction; 2) burrow and faecal pellet formation alters reaction and solute diffusion geometrics, creating a mosaic of biogeochemical microenvironments; 3) new reactive organic substrates in the form of mucus secretions may be introduced into the deposit independent of sedimentation processes; and 4) feeding and mechanical disturbance may influence microbial populations that mediate reactions." Hence the downward distribution of a

number of organisms affected by toxic reduced compounds, for example, metal sulphides (Theede et al., 1969) will be controlled by the bioturbatory activity of more tolerant organisms.

The macrobenthos stimulate rates of microbially mediated decomposition reactions (Aller, 1978; Yingst & Rhoads, 1980), providing enriched sediment for deposit feeders. This may occur through a number of different routes (Aller, 1982); the surface area of organic detritus is mechanically increased, grazing maintains microbial populations in a high-productivity phase of rapid growth, metabolite build-up is decreased and electron acceptor supply increased by irrigation, particle reworking and multidimensional diffusion, mucous secretions provide new reactive substrates and subduction or capture of resuspended reactive organic matter is increased during reworking.

The distribution of chemical gradients, particular grain sizes and local stability may thus be dependent on the presence or activity of certain organisms. These key primary species (as defined by Gray, 1974), which may occur as either dense assemblages of small individuals or less densely distributed larger individuals, can modify the sedimentary environment without self-exclusion. In doing so they control the distribution of secondary dependent species. These may in turn affect tertiary and quarternary, meiofaunal and microfaunal organisms which may also provide some feedback. An example of this overall process was described by Rhoads & Young (1971) in Cape Cod Bay, where the deep deposit feeding holothurian, Molpadia oolitica produces cone shaped faecal mounds, 10-30 cm in diameter with depressions in between filled with faecal pellets. The cones are not reingested so are relatively stable, and their surfaces were colonized and further stabilized by the tubiculous polychaete Euchone incolor. This allowed the further colonization by the bivalve Thyasira gouldi and the caprellid Aeginia longicornis. Faecal pellets in the depressions were readily resuspended

providing food for the suspension feeders on the cones. Thus considerable spatial heterogeneity of the bottom mud occurred, solely dependent on the burrowing habits of the holothurian.

The activity of large burrowing organisms has been highlighted for some time as a potential structuring force. They, "form a dominant component in the physical structure of the whole community ..... enhancing the survival of a considerable variety of small species." (Pearson & Rosenberg, 1978).

A considerable body of information has been contributed by palaeontologists and palaeoecologists. Soft bodied invertebrates are rarely preserved in the fossil record, but their traces often are. Observations of present day species have been used to hypothize about the modes of life of trace fossil producers. Schaefer (1972) has summarized much of this observational work in an encyclopaedic text based on the influence of organisms on the marine sediments of the southern North Sea. Work in this field has led to a better understanding of the evolution of marine benthic communities (Seilacher, 1977; Thayer, 1979) and some of the processes involved in their determination (Tevesz & McCall, 1983).

The largest members of the benthos were referred to as the megafauna by McIntyre (1971). He described them as sparsely distributed, scattered in patches or active on the deposit surface and normally not adequately sampled by conventional gear (dredges, grabs and cores). McIntyre applied the term to sand epifauna, but Atkinson (1986) extended the definition to include mud-burrowing decapod crustaceans and fish, partly differentiating between megafauna and macrofauna by the difference in respective burrow size.

Populations of these megafaunal burrowing organisms may themselves be subject to control. Primarily, there is a requirement for a sediment of a particular consistency, which is cohesive enough to support a burrow structure. They are also probably subject to a number of interactions including: intraspecific competition due to territoriality (for example within dense

populations of Calocaris macandreae - Gray, 1981), predation by demersal fish and stochastic events, for example fishing activity.

In British waters, the common sedimentary megafaunal burrowers and burrows have been described by Atkinson & Nash (1985). In soft sediments, this commonly includes the fish, Lesueurigobius friesii (Fries' goby), Lumpenus lampretaeformis (snake blenny) and Cepola rubescens (red band-fish) and the decapod crustaceans Nephrops norvegicus (Dublin Bay prawn or Norwegian lobster), C. macandreae and Callianassa subterranea. The last two are thalassinids, an exclusively burrowing group with a world wide distribution in intertidal and marine sediments. A number of other infrequently sampled megafaunal species occur in British waters.

Most of these species live beneath the normal sampling zone in the sediment, are very sparsely distributed or can avoid sampling gear (with the exception perhaps of C. macandreae). Little was known of their ecology or distribution until the advent of direct observation techniques, for example, underwater television and SCUBA diving (Atkinson & Nash, 1985).

C. macandreae does occur at high enough densities for its relatively shallow burrows to be regularly sampled by the use of remote grabs. Off the Northumberland coast, a population has been monitored for a period in excess of ten years (Buchanan, 1963b, 1974). The importance of this species in terms of community structure has been demonstrated by the constancy and stability of the population over time (17.95 individuals per square metre, coefficient of variation over ten years, 5.4%) and its ranking in the area as a biomass dominant (Buchanan, 1974; Buchanan & Warwick, 1974).

The largest obligate mud-burrowing crustacean in British waters, N. norvegicus, often co-occurs with C. macandreae and is widely distributed on the European continental shelf (Howard, 1982). This species supports a large sustainable commercial fishery. The U.K. fishery has a present annual catch

of 26,610 tonnes worth some £39.4 millions, 70% of which originates from Scottish waters (Anon, 1987).

The study presented in this thesis is an investigation of the interactions between megafaunal and macrofaunal species in soft sediments. The object was to identify and characterize the effects of megafaunal burrowing species both in terms of localized macrofaunal community structure, and in terms of the effects on individual species, suites of species and functional groups. The importance of megafaunal burrows in maintaining spatial heterogeneity in soft sediments is then discussed. The first part of this thesis (Chapters 2-4), is a progressive study to elucidate megafaunal effects and macrofaunal responses. Chapter 2 investigates four different sedimentary assemblages by both remote sampling and direct observation, to relate for the first time both megafaunal and macrofaunal community structure. The work carried out in Chapter 3 then describes one specific area in detail, to study on a much finer scale the physico-chemical and biological effects of burrow presence. This is repeated in further detail under the manipulative experimental conditions of sedimentary mesocosms in Chapter 4. Other experimental manipulations allowed 'real-time' interactions to be observed as they occurred.

The second part of this thesis (Chapter 5) is involved with the effect of organic enrichment on community structure along an enrichment gradient. This gradient, across the Garroch Head sludge dumping ground (Clyde Sea area, Scotland) has a well documented change in macrofaunal community structure (Pearson, 1986, 1987). Using underwater video, the megafaunal community structure is analysed along the same gradient and thus the effect on the macrofauna, of their exclusion from the high input end of the gradient, could be seen.

The final part (Chapter 6) draws together the principal threads of this study, in a general discussion of the factors determining heterogeneous community structure in soft sediments.

CHAPTER 2. MEGAFAUNAL/MACROFAUNAL COMMUNITIES

2.1 INTRODUCTION

Most megafaunal studies have been restricted to the biology and ecology of single species, for example, Calocaris macandreae (Buchanan, 1963b; Calderon-Perez, 1981) and Nephrops norvegicus (recently by Bailey et al., 1986). For N. norvegicus, studies of this nature have been principally related to the fishery. No studies have been undertaken into the relationship between local megafaunal burrowing species and macrofaunal species. Studies outside British waters have been detailed in Section 3.1.

In order to provide a baseline of information for further study, a range of megafaunal/macrofaunal assemblages were identified. In studying a range of sites, the effect of partial or full exclusion of megafauna on macrofaunal community structure could be seen. Two influences that can cause this exclusion are fishing activity and organic enrichment. The former has a direct effect on the megafauna by simple removal with relatively little effect on the macrofauna. The latter is more gradual and may have a direct effect on both assemblages.

Four sites were chosen from 'typical' west coast of Scotland sublittoral inshore soft sediments. Choice was made from previous knowledge of sites and by underwater surveys using a towed video sledge (see Chapter 5 for details of the video sledge). The principal criteria used in site selection were: a) accessibility for sampling, i.e. shallow enough for diving operations, and b) the presence of a megafaunal burrowing community. Three sites were selected in the Lynn of Lorne area near Oban and the fourth from the Clyde Sea area (see following section for full description). Two of the sites were situated in fjordic sea lochs and showed indications of natural organic enrichment, one with the additional input of an organic waste from an alginate processing factory. The two other sites were in close proximity, and were

thought to differ principally through the relative effects of fishing activity. The abundance of N. norvegicus had been considerably reduced at one of the sites by trawling, so it was used as a control area for comparison with the adjacent well burrowed site. It was thought that without these external factors of fishing activity and organic enrichment, the sites would have generally similar macrofaunal composition. Macrofaunal abundance would, however, differ between sites, due to differing local conditions.

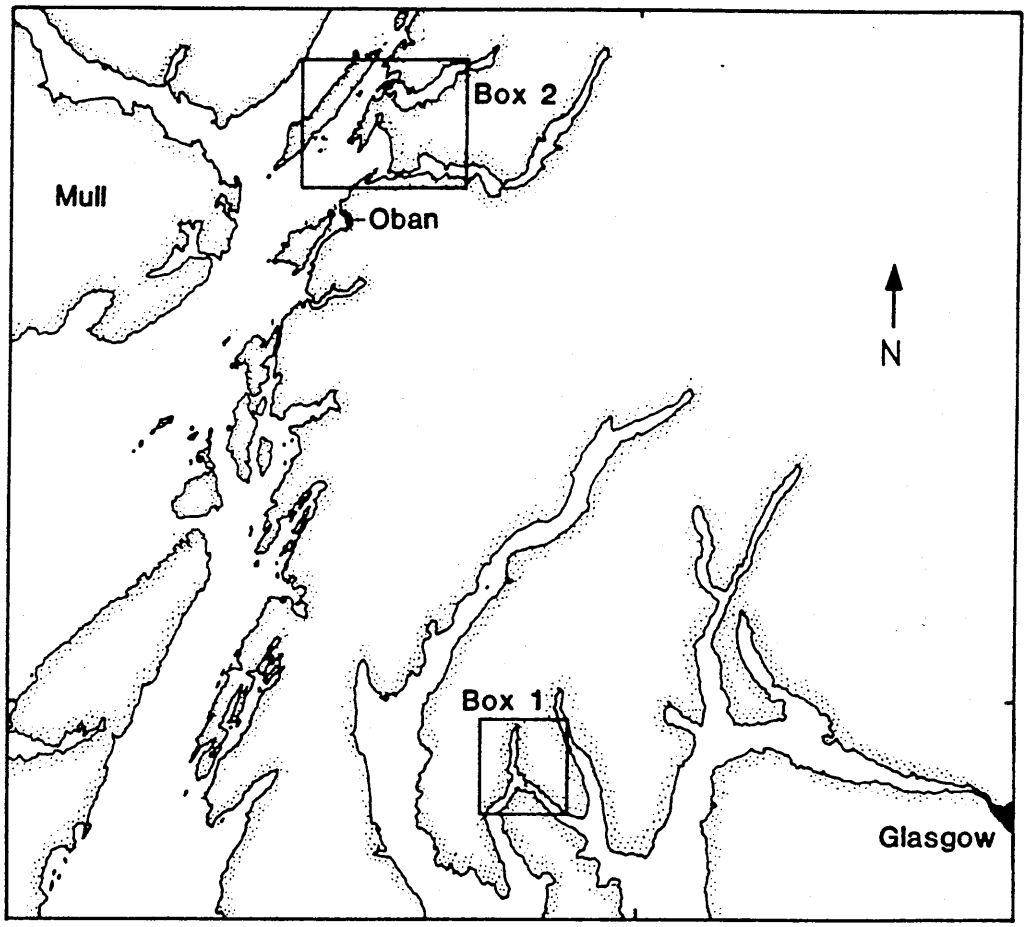
As described below, each site was studied by remote macrofaunal sampling linked with diver transects to estimate megafaunal composition and abundance. Comparison of sites allowed assessment of the probable importance of megafaunal burrowing species in affecting benthic community structure.

2.2 SAMPLE STATIONS

The two main sampling areas are shown in Fig. 2.1. They were a sea loch area in the Firth of Lorne near Oban and the Loch Riddon area in the Clyde Sea.

2.2.1 Loch Riddon Site

The Loch Riddon sampling site was situated in the north west corner of Fearnoch Bay (55°56.30'N, 5°10.80'W; Ordnance survey grid reference NSO12762, see Fig. 2.1, Box 1) of Loch Riddon, in approximately 23 m of water on a gently shelving mud bank. The sediment was of a heterogeneous nature with a high silt-clay content, sandier towards both the shore and the entrance to the bay. This was burrowed mostly by N. norvegicus in water below 20 m depth and by the amphipod Maera loveni in shallower waters. Epifaunal species present included various species of opisthobranch mollusc, decapod and echinoderms, for example Buccinum undatum, Liocarcinus puber and Asterias rubens. Water clarity was generally poor due to the generally



Box 1 Clyde Sea area sample site.

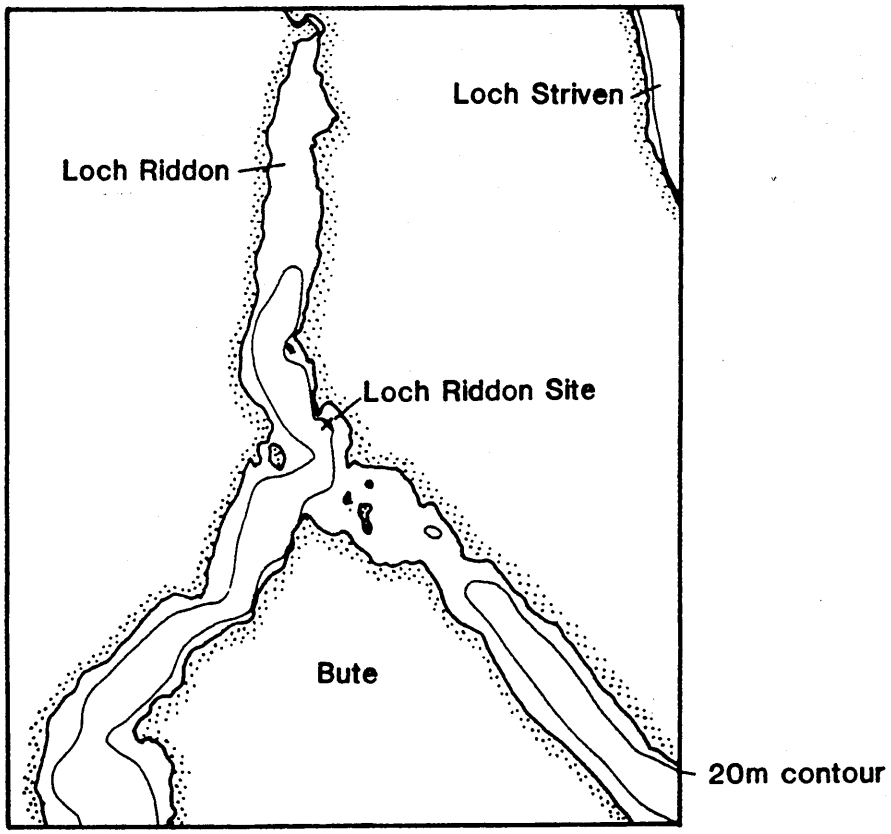
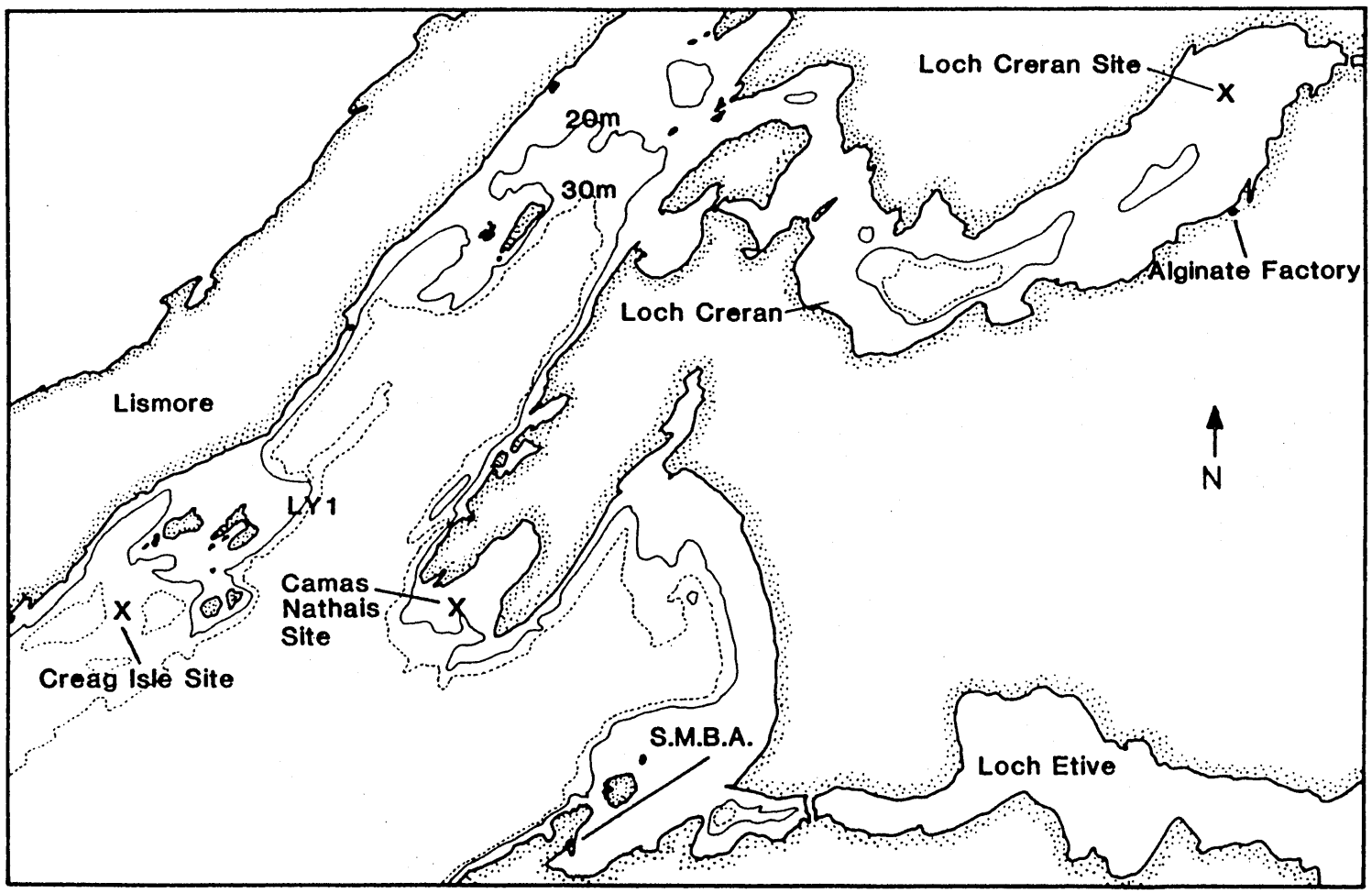


Figure 2.1 continued. Box 2: Firth of Lorne area sample sites.



turbid nature of the loch. High fluvial input from the surrounding hillsides was often responsible for a dark peaty layer of fresh water on the top of the more marine loch water. This input was also responsible for a considerable amount of detritus noted in and on the sediment, mostly in the form of terrestrial matter but also including some fragments of detached littoral macroalgae. As well as littoral and fluvial inputs two fish farms in the vicinity may also influence the area. In a recently published survey (Pearson et al., 1986a), it has been reported that benthic populations of the inner sea lochs of the Clyde Sea are markedly enriched. It was suggested that this enrichment may be caused by a general eutrophication of the Clyde Sea area brought about by high nutrient inputs.

2.2.2 Loch Creran Site

The Loch Creran sampling site was positioned towards the head of the lower loch (56°32.35'N, 5°19.00'W; Ordnance Survey grid reference NM963436, see Fig. 2.1, Box 2). Like most Scottish sea lochs, Loch Creran originated as a submerged glaciated river valley (Ansell, 1974). It has an upper and lower basin, which are separated by a narrow, shallow sill. The site was situated in a large relatively shallow area below the dividing sill in approximately 16 m of water. The substratum consisted of a very soft unconsolidated silty sediment. Large visible immobile epifauna included the pennatulid Virgularia mirabilis, large cerianthid anemonies (mostly Cerianthus lloydii) and the sabellid polychaetes Sabella pavonina and Myxicola infundibulum. Mobile epifauna observed in the vicinity was similar to that of the Loch Riddon site. Areas of burrowed sediment were patchy but included characteristic callianassid-type mounds (Atkinson & Nash, 1985) and burrows of the crustacean N. norvegicus and the fish Lesueurigobius friesii. The general hydrography of the loch has previously been studied by Gage (1972), Ansell (1974) and Tett & Wallis (1978). The study by Gage (1972) was a

detailed survey of the macrofauna at a number of sites in the loch. It was noted that the loch receives a large fresh water input and that surface water salinities could be considerably reduced.

The loch is open to prevailing south-westerly winds and due to the shallowness of the soft bottom a large amount of material may be resuspended during winter storms (Ansell, 1974). Thus, with turbulent mixing of the surface peaty layer, visibility can easily be reduced.

Besides the fluvial and littoral inputs, the other major source influencing the loch is the effluent from an alginate processing factory at Barcaldine (see Fig. 2.1, Box 2), approximately 1.2 km distant from the sampling site, across open water. This effluent contains a large amount of dissolved and particulate organic matter and has been discussed in terms of the overall carbon budget of the loch by Tyler (1983). The localized effects of the effluent on macrofaunal community structure have been studied by Pearson & Stanley (1977).

2.2.3 Camas Nathais Site

The Camas Nathais sample site (56°28.70'N, 5°27.90'W; Ordnance Survey grid reference NM867373, see Fig. 2.1, Box 2) was situated between the two headlands of the bay, in approximately 22 m. The sea bed consisted of a soft flat sediment which was occasionally seen to be covered with a visible layer of diatoms. The sediment was well consolidated below 5 cm depth with a broken shell layer (mostly fragments of the gastropod Turritella communis) becoming more clay-like with increasing sediment depth. Towards the head of the bay sediments were of a sandier nature. Mobile epifaunal species were similar to those at the other sites. The sediment had a dense covering of the pennatulid V. mirabilis, most of which were less than 5.0 cm high. Megafaunal burrows were sparse when compared to the other sites but C. macandreae and N. norvegicus were present. Direct fluvial and littoral inputs were thought to be negligible in the area. Although flushing from Loch Etive may affect the

Bay, the site was thought to be under the same general hydrographic conditions as the Lynn of Lorne.

This site was heavily fished commercially for N. norvegicus. Just prior to the placement of the site marker buoy, a fishing boat trawled in and out of the bay for several days taking a large catch (exact extent unknown). Trawl marks were observed by divers on the sediment surface. During the period of study at this site, there was continual creeling in the vicinity of the entrance to the bay. At least two fleets of creels (single buoyed ground lines with approximately 30 creels attached to each) were in operation in the area over much of the study period.

2.2.4 Creag Isle Site

The Creag Isle site (56°28.52'N, 5°32.00'W; Ordnance Survey grid reference NM824371, see Fig. 2.1, Box 2) was situated approximately half way between Creag Isle and Rubha na Gaoith on Lismore. The site was centred on a small plateau in 26 m surrounded by deeper water. The sea bed was a soft flat sediment very similar in consistency to that of Camas Nathais. The surface was penetrated by numerous burrow openings, mostly those of C. macandreae. The commonest epifaunal species was the pennatulid Pennatula phosphorea with a few large individuals of the related Funiculina quadrangularis also present. Mobile epifauna were similar to those of the other sites except for the presence of a number of individuals of the squat lobster Munida rugosa observed in the openings of burrows belonging to N. norvegicus.

The site was sheltered somewhat from prevailing winds by Lismore and this, coupled with the depth of water, was thought to negate the effects of surface turbulence on the sea-bed when compared with the other sites. Bottom currents experienced by divers were strongest at this site and water clarity could reach several metres visibility in good conditions. There were no

major terrestrial influences and it was thought the general hydrographic conditions of the Lynn of Lorne area also prevailed at this site. Owing to the presence of deeper bouldery sediments, the site was unsuitable for trawling. However, a small amount of creeling was evident in the area during the study period.

A number of sites in the Loch Creran and Lynn of Lorne area (see LY1 in Fig. 2.1, Box 2) have been investigated as part of a long term study of hydrography, nutrient and phytoplankton levels (Grantham, 1981, 1983; Grantham et al., 1983). Long term changes in the macrobenthos have also been investigated at the LY1 site by Pearson et al. (1982, 1986b).

2.3 METHODS AND MATERIALS

2.3.1 Analysis of Macrobenthic community

Samples were taken using an 0.1 m^2 van Veen grab. Five replicate grabs were taken at each station. Each sample was wet sieved (mesh size 1.00 mm) to remove sediment, then fixed in 4% buffered formalin in sea water with Rose Bengal added. The latter, a vital stain, facilitated easy sorting as all living tissue was dyed red. Samples were eye sorted, wet weighed in major groups and the macrofauna enumerated and identified to species level where possible. The taxonomic keys used for the identification of species are shown in Appendix 1.

2.3.2 Analysis of Sedimentary Characteristics

At the same time as the macrofaunal samples were taken, an extra grab was taken for sediment analysis., A small sub-sample was removed, sealed in a bag and deep frozen for storage prior to analysis. Particle size analysis was carried out by a combination of dry sieving and pipette analysis, according to

Buchanan (1984) and Folk (1974). The organic content of the sediment was estimated by the chromic acid oxidation technique of Walkley & Black (1934). This method is more accurate than that of weight loss by ignition (Buchanan, 1984).

2.3.3 Analysis of Megafaunal Community

The megafaunal species and abundance were estimated at each site by diver transects. The method was identical for each site. A 25 m long weighted marker line was laid straight on the sea bed. The line was tagged at metre intervals. The same diver then went along the transect line with a square metre quadrat, recording all features within the quadrat on a slate. This was done at each metre interval on both sides of the line. Connections between burrow openings were determined by the use of a flexible water bottle and hose. The hose was introduced into a burrow opening and the bottle squeezed. All flumes of sediment coming from other openings were recorded as being from the same system. Burrow types were fairly distinctive having been mostly described in Atkinson & Nash (1985) and Atkinson (1986) and could be ascribed fairly accurately to a particular species. Observations were made at each site over a period of days, the extent of area covered depending on the depth of water and consequently the bottom time available to the diver.

The extent of burrowing below the sediment surface was determined by resin casting a number of representative burrows of each megafaunal species. The method used was that described by Atkinson & Chapman (1984). Preactivated polyester resin (Trylon U.K.; SP701PA low viscosity lay-up resin with a cobalt accelerator) was mixed on site with an organic peroxide catalyst (1.5%) and lowered to the sea-bed where divers poured it into burrows. Bottomless 1 litre sample buckets were previously placed over the burrow openings to provide a hydraulic head of resin to the burrows. Casts were left

to cure overnight and were removed by careful excavation by hand the following day. Further curing took place in fresh air.

Several measurements were made of each cast. Surface area was determined by wrapping each cast in a monolayer of aluminium foil of known weight per unit area and by weighing the total amount of foil used. The cast volumes were calculated from the weight of the burrow complex and the specific gravity of the resin (1.21 in the case of SP701PA). Tunnel height and width were measured with vernier callipers.

2.3.4 Data Analysis

Random collection of samples by remote sampling allows valid statistical comparisons of animal abundances and of physico-chemical variations. However, benthic fauna are rarely randomly distributed (Gray, 1981), but rather are discretely distributed in patches. Normal distributions are a pre-requisite for parametric data analysis. Transforming the original data, for example, to log(x+1) may 'flatten' the data and hide more subtle differences. It is preferable, therefore, to use non-parametric statistics which, although not as powerful as parametric techniques, are adequate for the present comparative purposes. The Kruskal-Wallis test was used to compare the mean abundances across the sites. This is the non-parametric equivalent of one-way analysis of variance and has a power efficiency of about 95% (Elliot, 1977). In Chapters 3 and 4, the Mann-Whitney U-test was used to compare sample statistics instead of the parametric t-test, and the test for equal variances was used to analyse differences in variance between redox core profiles and core penetration depths. The Chi-squared test was used for agreement between observations and hypotheses, where the hypothesis specifies that proportions or probabilities of a series of observations fall into several groups, for example, the percentage composition of faunal groups. These tests are described in Elliot (1977) and Conover (1980).

Simple analysis of community structure was based on the parameter statistics of species number (S), abundance (A) and biomass (B). Abnormal environmental variability in either space or time may disturb community stability and will be reflected in these basic parameters (Pearson & Rosenberg, 1978). Two further statistics were derived from these parameters. The abundance ratio (A/S) refers to the average number of individuals per species, whilst the size ratio (B/A) indicates the average weight per individual (Pearson et al., 1982).

For graphic analysis of community structure, a K-dominance plot was used (Lambshead et al., 1983). The distribution of individuals amongst species has been fitted to mathematical functions supporting resource apportioning models (Whittaker, 1975; May, 1976; Gray, 1981; Hughes, 1984). Small samples with a limited number of species, long life cycles and stable populations may conform to random niche or broken stick models (MacArthur, 1957). Samples with a higher number of species with dominants constituting a large proportion of the community may conform to a geometric (logarithmic) series. This is more appropriate for benthic communities as response to environmental factors is geometric not linear, i.e. adverse conditions would cause a decrease by a fraction of the population present and not by a given number of individuals. Samples (either heterogeneous or homogeneous) that are very rich in species number, from a range of environments and communities, tend to fit a log normal distribution.

Hughes (1984), however, has criticized the fitting of logarithmic distributions to marine benthic communities. Log-normal plots are now more often used to assess degrees of dominance within communities. Shaw et al. (1983) suggested that alternatively, a simple assessment of dominance might prove better in detecting disturbed or polluted faunal assemblages. They also suggested that although ranked species abundance curves were a sensitive means of detecting differences in dominance patterns, a simple index would be

more convenient to use. Lambshead et al. (1983) developed this idea further. They looked at not just the dominance of the most abundant species but also considered the combined dominance of the two most abundant, three most abundant, etc., to the K^{th} most abundant species, plotting this as a K-dominance curve.

Multivariate analysis was used to further compare the sample sites in terms of the presence of the most dominant species. The Jaccard coefficient was calculated to indicate the degree of similarity between sites.

Polychaete trophic groups were analysed using information summarized principally in Fauchald & Jumars (1979) but also in Pearson (1971) and Gaston (1987), with some modification in this study by the addition of an omnivore/scavenger group.

2.4 Results

2.4.1 Macrofaunal Community Structure

The full list of species identified with their abundances is shown in Table 2.1. Each column represents one of the sampling sites. The figures in these columns are the abundance of each species averaged across 5 replicate 0.1 m^2 grab samples. The last column refers to the polychaete feeding guilds and is explained further on in this section. Fourteen identifiable species occurred at all the sites. These were: the polychaetes Pholoe minuta, Prionospio malmgreni, Chaetozone setosa, Diplocirrus glaucus, Scalibregma inflatum, Notomastus latericeus, Rhodine gracilior, Amaeana trilobata and Terebellides stroemi, the bivalves Mysella bidentata, Abra nitida and Corbula gibba, the phoronid Phoronis muelleri and the ophiuroid Amphiura filiformis. Twenty two species co-occurred at 3 sites, 21 species at 2 sites and 57 species occurred at only one site.

Table 2.1 Species collected from the four sample sites. Values are for mean abundance per square metre. Polychaete feeding guilds have been assessed and are explained in the following text.

	Loch Creran	Loch Riddon	Camas Nathais	Creag Isle	Polychaete Feeding Guild
Protozoa					
Foraminifera Type 1			358	22	
Coelenterata					
Cerianthus spp.	2			6	
Pennatula phosphorea (L.)			8	10	
Virgularia mirabilis (Muller)	14		214	2	
Varia					
Platyhelminthes Type 1		6			
Type 2		2			
Nematoda spp.		4			
Nemertea Type 1	20	68	4		
Type 2	2	12	4		
Annelida					
Aphrodita aculeata L.		2			CMJ
Harmothoe sp.		6			CMJ
Pholoe minuta (Fabricus)	66	34	32	2	CMJ
Eumida sanguinea (Oersted)			2	2	CMX
Ophiodromus flexuosus (delle Chiajei)	8	16		6	CMJ
Ancistrosyllis groenlandica McIntosh			2		CMJ
Langerhansia cornuta Rathke			10		CMJ
Syllis sp.			2		CMJ
Exogene sp.			2		VMJ
Nereidae sp.		2			VMJ
Nephtys hombergii Savigny		46	80	104	VMJ
Nephtys hystricus McIntosh	70				VMJ
Glycera alba (Muller)	2	22		4	CDJ
Glycera convoluta Keferstein			4		CDJ
Glycera rouxi Andouin and Milne-Edwards		2			CDJ
Glycera spp.		4			CDJ
Goniada maculata Oersted		90			CDJ

Table 2.1 (continued)

	Loch Creran	Loch Riddon	Camais Nathais	Creag Isle	Polychaete Feeding Guild
Lumbrineris hibernica (McIntosh)	38		82	10	CMJ
Scoloplos armiger (Muller)	16	166			BMX
Spiophanes kroyeri Grube		114	16	14	SDT
Polydora sp.	14	6	6		SDT
Prionospio malmgreni Claparede	24	14	4	10	SDT
Prionospio sp.		8			SDT
Magelona filiformis Wilson			20	2	SDT
Apistobranchus tullbergi (Theel)	1134				SDT
Levinsenia gracilis (Tauber)	20		8		SMX
Cirratulus filiformis Keferstein			72	6	SDT
Tharyx marioni (Saint-Joseph)	4				SDT
Tharyx multibranchiis (Grube)		2		4	SDT
Chaetozone setosa Malmgren	4	18	2	2	SDT
Yellow cirratulid		2			SDT
Diplocirrus glaucus (Malmgren)	10	336	12	20	SDT
Scalibregma inflatum Rathke	184	36	58	2	BMX
Ophelina acuminata Oersted		6			BMX
Notomastus latericeus Sars	24	8	32	2	BMX
Dasybranchus caducus (Grube)				2	BMX
Capitomastus minimus (Langerhans)	2				BMX
Capitellidae spp.	2				BMX
Rhodine gracilior Tauber	48	22	66	26	BLX
Praxillella gracilis (Sars)		6	30	38	BLX
Maldanidae spp.	2	10	2	14	BLX
Owenia fusiformis delle Chiajei		8			FDT
Amphictene auricoma (Muller)		86			BMX
Pectinariidae sp.			4		BMX
Ampharete grubei Malmgren		2	6	6	SLT
Melinna palmata Grube	522	38	62		SLT
Amphitrite variablis (Risso)			2		SLT
Amphitrite cirrata (O.F. Muller)		2			SLT

Table 2.1 (continued)

	Loch Creran	Loch Riddon	Camas Nathais	Creag Isle	Polychaete Feeding Guild
Proclea graffi (Langerhans)		6			SDT
Amaeana trilobata (Sars)	64	20	70	2	SDT
Lysilla loveni Malmgren		2			SDT
Trichobranchus glacialis Malmgren		8			SLT
Terebellides stroemi Sars	4	34	6	10	SLT
Terebellidae sp.				2	SLT
Sabellidae sp.	10	2			FLT
Oligochaete sp.			2		
Sipunculida					
Golfingia elongata (Keferstein)			14	12	
Phascolion strombi (Montagu)		2	32		
Crustacea					
Cumacea sp.		4	2	16	
Tanaid sp.		4			
Gnathia maxillaris (Montagu)			6		
Isopod spp.	2				
Amphipod Type 1	42	6	6	14	
Type 2	8	2	14	6	
Type 3	2	2	4		
Type 4			4		
Euphausiacea spp.	4				
Mollusca					
Chaetoderma nitidulum Loven		4	2	6	
Turritella communis Risso		2	132	108	
Capulus ungaricus (L.)				2	
Lunatia poliana (delle Chiajei)		10			
Mangelia brachystoma (Philippi)			12		
Prosobranchia sp.	4				
Brachystomia lukisii Jeffreys			2		
Retusa umbilicata (Montagu)	18	106	2		
Philine aperta (L.)		10			
Nuculoma tenuis (Montagu)		14			

Table 2.1 (continued)

	Loch Creran	Loch Riddon	Camas Nathais	Creag Isle	Polychaete Feeding Guilds
Nucula sp.		32	4	6	
Modiolus modiolus (L.)		4			
Limatula sulcata (Leach in Brown)				2	2
Cyprina islandica (L.)		12		2	
Thyasira flexuosa (Montagu)	52	694		4	
Myrtea spinifera (Montagu)	2		4		
Neolepton sulcatulum (Jeffreys)		2			
Mysella bidentata (Montagu)	604	150	298	74	
Acanthocardia spp.			4		
Dosinia lupinus (L.)		2	8		
Gouldia minima (Montagu)			2		
Abra alba (Wood)	14	4			
Abra nitida (Muller)	8	40	10	8	
Abra sp.	54				
Phaxas pellucidus (Pennant)			22	2	
Corbula gibba (Olivi)	4	2	102	194	
Mya truncata (L.)	2	26	28		
Thracia convexa (Wood)	4	62			
Thracia pubescens (Pulteney)		6			
Varia					
Terebratulina retusa (L.)			8		
Phoronis muelleri Selys-Longchamps	6	54	10	14	
Sagitta elegans Verrill		2			
Echinodermata					
Amphiura chiajei Forbes	36		42	48	
Amphiura filiformis (Muller)	84	88	52	22	
Ophiura ophiura (L.)	2				
Ophiura affinis Lutken			2		
Ophiura spp.		34			
Echinocardium cordatum (Pennant)		2			
Trachythyone elongata (Duben and Koren)		4		2	
Thyone spp.			2		
Holothuroidea sp.	2	2			

The dominant species with abundances in excess of 100 m^{-2} were abstracted and are shown in Table 2.2. Three of the top four species were from the Loch Creran sample site, Apistobranchus tullbergi, M. bidentata and Melinna palmata. The former did not occur at any of the other sites. There were significant differences in the mean abundance between the sample sites, for all the ranked species (Kruskal-Wallis test, $P < 0.05$).

The 10 dominant species from each site are shown with their abundances and percentage abundance (dominance) in Table 2.3. The percentage abundance was used to plot the K-dominance curves for each site. As previously stated, Loch Creran was dominated by the polychaete A. tullbergi. The other dominants were mostly polychaetes, but also included a number of bivalves and an echinoderm. The Loch Riddon and Creag Isle sites were dominated by the bivalves Thyasira flexuosa and Corbula gibba respectively, the Camas Nathais site by an agglutinating foraminiferan. These last three sites contained dominants from a variety of groups including polychaetes, bivalves, echinoderms, gastropods, opistobranchs, nemerteans, foraminiferans and pennatulids. Only one species, the bivalve M. bidentata was a dominant at all four sites.

A percentage similarity matrix was erected based on the Jaccard coefficient, using the presence and absence of the 10 most dominant species found at each site. Overall 26 species were represented.

	Loch Creran	Loch Riddon	Camas Nathais	Creag Isle
Loch Creran	-	-	-	-
Loch Riddon	62.5	-	-	-
Camas Nathais	66.7	64.0	-	-
Creag Isle	58.3	56.0	81.8	-

Table 2.2 Numerically dominant species found at the Sample Sites.

(Abundance > 100 m^{-2} at any one site).

SPECIES	Loch Creran	Loch Riddon	Camas Nathais	Creag Isle
Apistobranchus tullbergi	1134	-	-	-
Thyasira flexuosa	52	694	-	4
Mysella bidentata	604	150	298	22
Melinna palmata	522	38	62	-
Foraminifera Type 1	-	-	358	22
Diplocirrus glaucus	10	336	12	20
Virgularia mirabilis	14	-	214	2
Corbula gibba	4	2	102	194
Scalibregma inflatum	184	36	58	2
Scoloplos armiger	16	166	-	-
Turritella communis	-	2	132	108
Spiophanes kroyeri	-	114	16	14
Nephtys spp.	70	46	80	104
Retusa umbilicata	18	106	2	-

Table 2.3 The 10 most dominant species from each sample site, with percentage dominance.

	No/m^2	%
LOCH CRERAN		
Apistobranchus tullbergi	1134	34.7
Mysella bidentata	604	18.5
Melinna palmata	522	16.0
Scalibregma inflatum	184	5.6
Amphiura filiformis	84	2.6
Nephtys hystricus	70	2.1
Pholoe minuta	66	2.0
Amaeana trilobata	64	2.0
Abra sp.	54	1.6
Thyasira flexuosa	52	1.6
LOCH RIDDON		
Thyasira flexuosa	694	26.0
Diplocirrus glaucus	336	12.6
Scoloplos armiger	166	6.2
Mysella bidentata	150	5.6
Spiophanes kroyeri	114	44.3
Retusa umbilicata	106	4.0
Goniada maculata	90	3.4
Amphiura filiformis	88	3.3
Amphictene auricoma	86	3.2
Nemertea Type 1	68	2.6
CAMAS NATHAIS		
Foraminifera Type 1	358	16.9
Mysella bidentata	298	14.1
Virgularia mirabilis	214	10.1
Turritella communis	132	6.2
Corbula gibba	102	4.8
Lumbrineris hibernica	82	3.9
Nephtys hombergii	80	3.8
Cirratulus filiformis	72	3.4
Amaeana trilobata	70	3.3
Rhodine gracilior	66	3.1
CREAG ISLE		
Corbula gibba	194	22.6
Turritella communis	108	12.6
Nephtys hombergii	104	12.1
Mysella bidentata	74	8.6
Amphiura chiajei	48	5.6
Praxiella affinis	38	4.4
Rhodine gracilior	26	3.0
Foraminifera Type 1	22	2.6
Amphiura filiformis	22	2.6
Diplocirrus glaucus	20	2.3

Based solely on the more dominant species, the Creag Isle and Camas Nathais sites showed the greatest similarity, the Creag Isle and Loch Riddon sites were the least similar. There was an intermediate level of similarity between the Loch Creran, Loch Riddon and Camas Nathais sites. No realistic levels of significance could, however, be attached to these similarities.

Table 2.4 features the major community parameters for each site. These are: total species number, average species number, abundance, biomass, abundance ratio, size ratio, Shannon-Wiener diversity index and Pielou index of evenness. Species number (S), abundance (A), biomass (B), abundance ratio (A/S) and size ratio (B/A) are compared graphically in Figure 2.2.

Total and average species number was highest in Loch Riddon (73 and 39.4 respectively), Camas Nathais was fairly similar (64 and 36.8). Lower species numbers were recorded at the Loch Creran and Creag Isle sites. Abundance was highest at the Loch Creran site (3264 m^{-2}) largely consisting of A. tullbergi. The site with least abundance was Creag Isle with only 872 individuals m^{-2}. Biomass was highest at the Loch Creran site (220 gm^{-2}), twice as high as at any of the other sites. Creag Isle had the second highest biomass of 116.7 gm^{-2}. The abundance ratio was considerably higher at the Creag Isle site, a function of the low species number there. The greatest size ratio was also exhibited at the Creag Isle site; individuals were twice as large (wet weight) as those at the Loch Creran site and 3.5 times larger than at the other two sites. With the heavy gastropod Turritella communis removed from the calculations, the value for the size ratio at the Creag Isle site was still higher than at the other sites (0.09 g per individual).

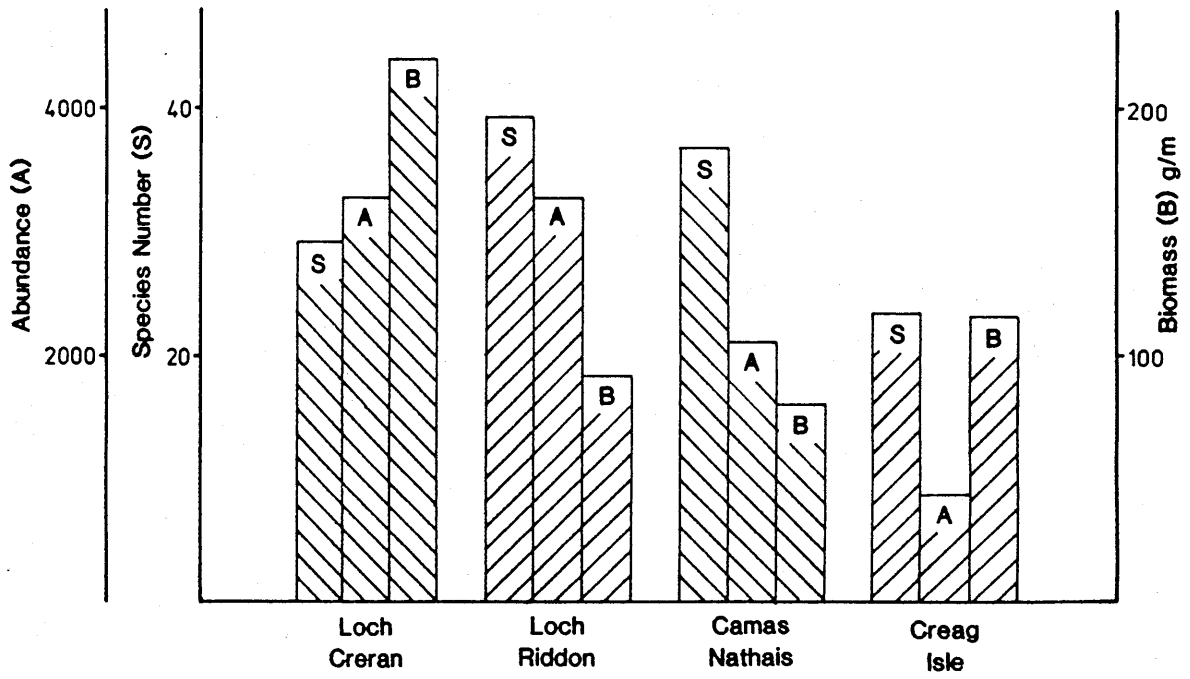
Individual significant differences were exhibited across all the sites for species number, abundance, biomass, abundance ratio and size ratio ($P < 0.05$).

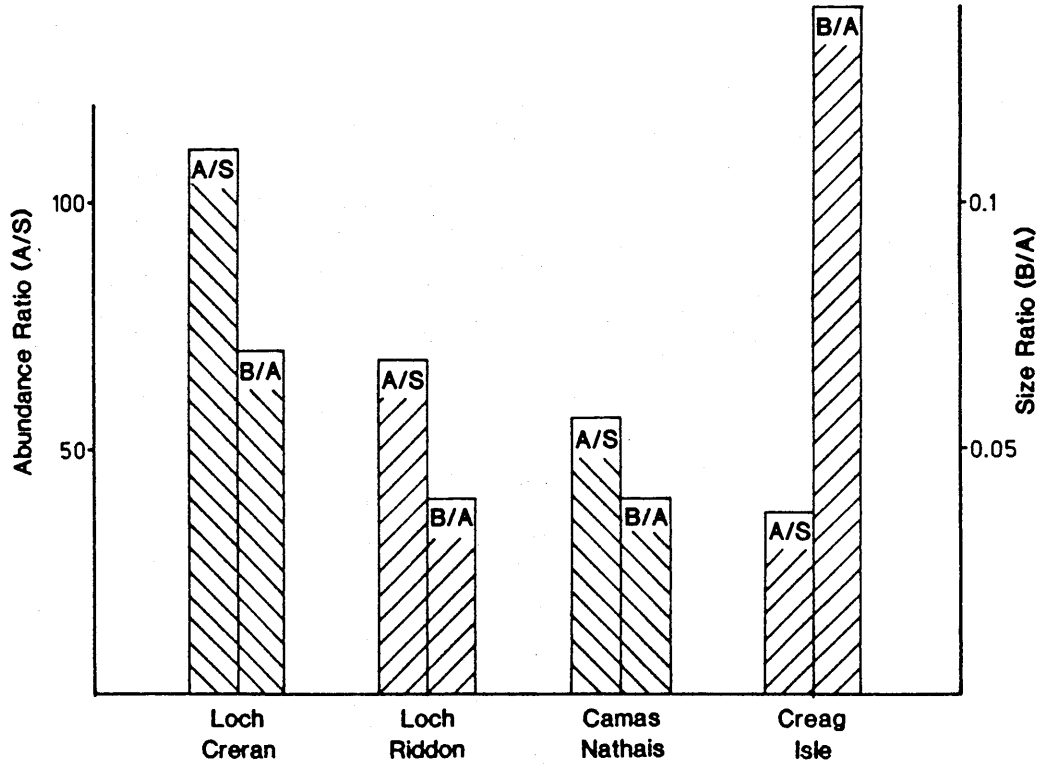
The Shannon-Wienner index indicated that the Camas Nathais site was the most diverse (the greater the index, the more diverse a site is), with the Loch Riddon site fairly similar (4.49 and 4.38 respectively). The Loch Creran

Table 2.4 Major community statistics for each sample site (per m^2), including total number of species found (S_T), mean number of species (S_A), mean abundance (A), biomass (B), abundance ratio ($^A/S$), size ratio ($^B/A$), Shannon-Wiener diversity index (H') and Pielou index of evenness (E). Mean values are from 5 replicates. Levels of significance are: * = $P < 0.001$, + = $P < 0.05$, N.S. = no significant difference between sample sites.

	S_T	S_A	A	B	$^A/S$	$^B/A$	H'	E
Loch Creran	48	29.2	3264	220	111.8	0.07	3.29	0.19
Loch Riddon	73	39.4	2678	92.3	68.5	0.04	4.38	0.27
Camas Nathais	64	36.8	2114	80.9	56.5	0.04	4.49	0.34
Creag Isle	46	23.6	872	116.7	36.9	0.14	4.14	0.37
Significance	N.S.	*	*	+	*	*	N.S.	N.S.

Figure 2.2 Comparison of species number (S), abundance (A), biomass (B), abundance ratio (A/S) and size ratio between the different sample sites. Values are per square metre.





site was the least diverse with a value of 3.29. Pielou evenness index gave a measure of the evenness of the distribution of individuals amongst the species. The index tends to +1.0 for maximum evenness and 0.0 for minimum evenness. Loch Creran was the least even site (0.19), Creag Isle the most even (0.37).

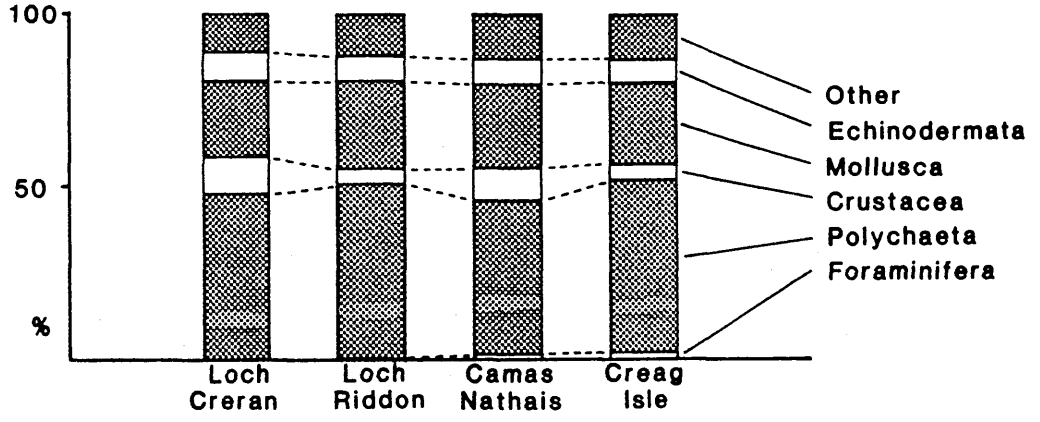
The composition of the major faunal groups for the species number, abundance and biomass are shown in Figure 2.3. Species composition was similar between all the sites and proportions were constant, with no significant differences between sites. Polychaetes made up over 45% of the species composition at each site, Mollusca over 22%. The other groups shown were Crustacea, Echinodermata, Foraminifera and 'Other Fauna' (this latter group included nemerteans, nematodes, oligochaetes etc.).

In terms of abundance, there was a highly significant difference ($P < 0.001$) in composition between sites. Mollusca and Polychaeta made up the greatest number of individuals at all sites. Polychaetes were particularly abundant at the Loch Creran site (69.6%) and ranged between 33% and 44% of the abundance at the other sites. Mollusca made up the greatest proportion of the Creag Isle site (47%) and less so at the other sites. Foraminifera were only found at two of the sites and although only one species was recorded, the agglutinating Type 1 species, this made up 17% of the total abundance at Camas Nathais.

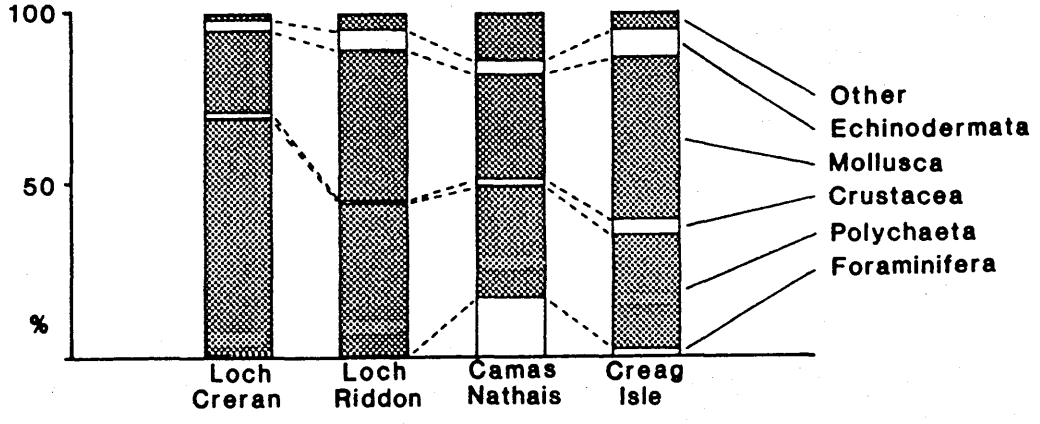
A highly significant difference ($P < 0.001$) was exhibited by the biomass composition between sites. The biomass of Loch Creran was made up largely of sedentary polychaetes (65%), in particular the ampharetid Melinna palmata. This species was collected in its tube and was weighed along with the part of the tube immediately surrounding the animal, adding considerably to its biomass. The biomass composition of the Loch Riddon site was also made up largely by sedentary polychaetes (74.2%). Generally, these polychaetes (in particular the terebellids) were large with high individual biomass. There was a more even distribution of biomass amongst the major groups at the two other

Figure 2.3 Percentage composition of species number, abundance and biomass for each of the sample sites.

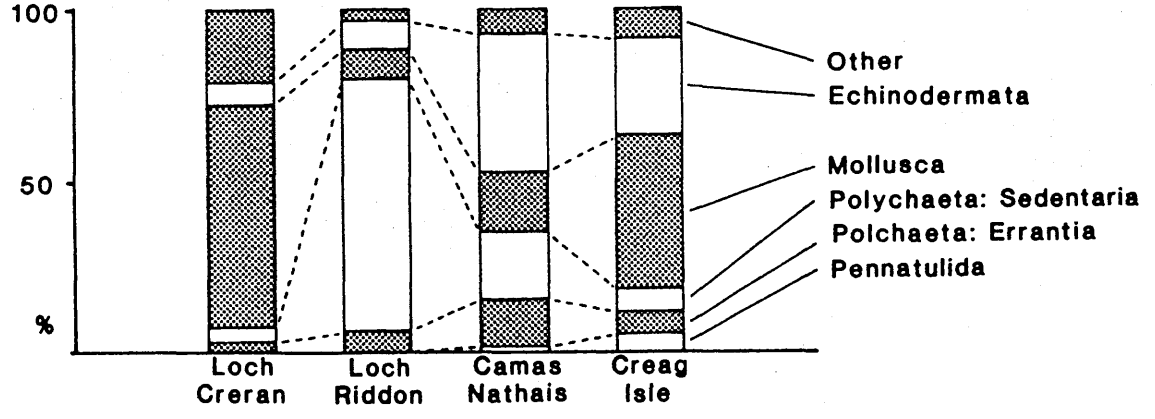
1. Species Number



2. Abundance



3.Biomass

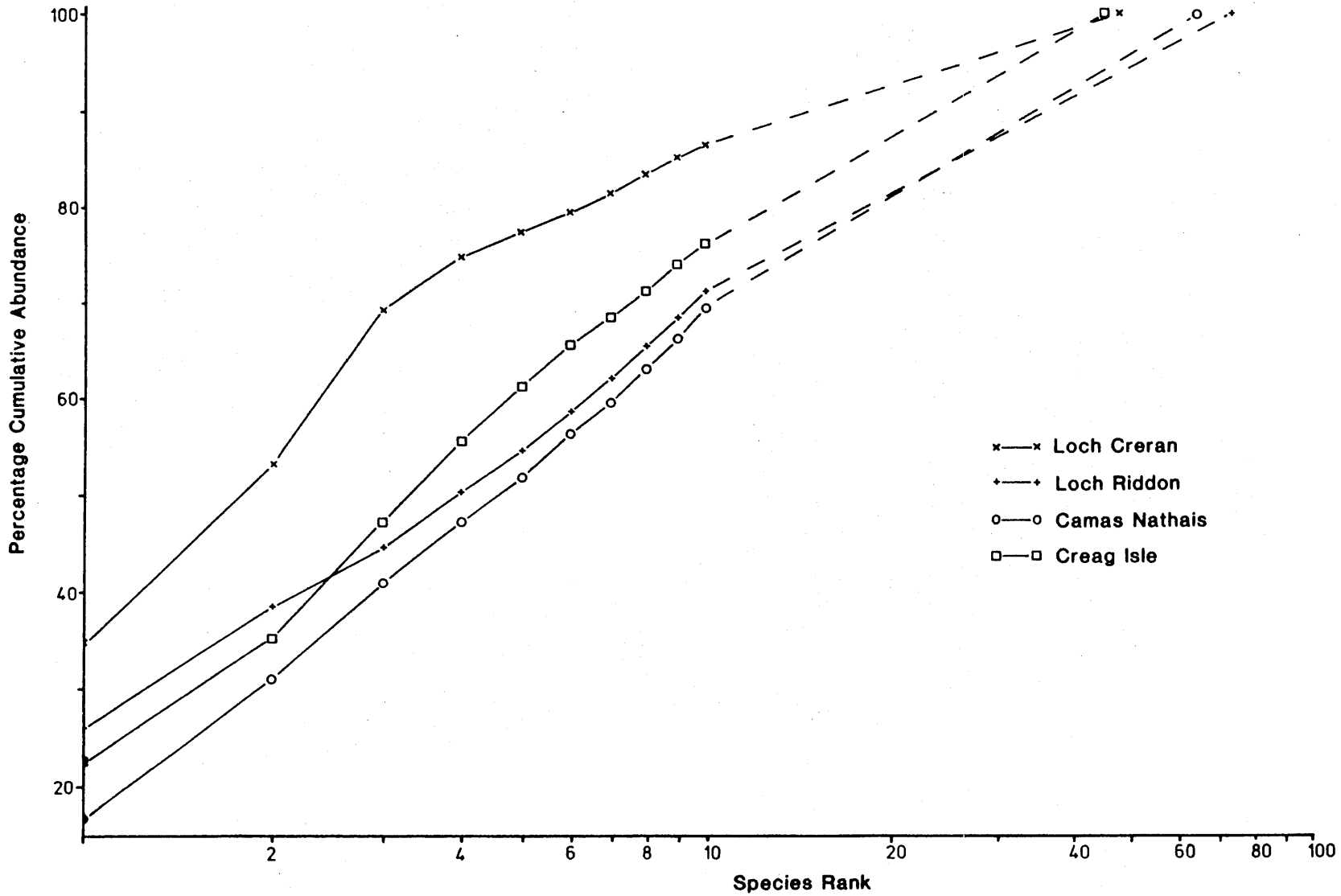


sites. Of these, echinoderms accounted for a large proportion of the biomass at both the sites whilst Mollusca dominated at the Creag Isle site (45.7%). This latter group was almost entirely made up of large numbers of the heavy shelled gastropod Turritella communis. Pennatulids made up 6.5% of the biomass at Creag Isle and approximately half this at the Loch Creran and Camas Nathais sites. No pennatulids were recorded from the Loch Riddon site.

Differences in community structure between the sampling sites were assessed graphically in Fig. 2.4, the K-dominance plot. The x-axis represented the species rank in order of greatest abundance on a log scale, the y-axis the percentage cumulative abundance. The nearer the curve to the top left hand corner, the greater the degree of dominance exhibited by that community. The nearer the curve to the lower right corner the more diverse that community was. The curve for Camas Nathais exhibited the greatest overall diversity as it was lower than the curves for the Loch Creran and Creag Isle sites. The curve for Loch Riddon crossed over that of Creag Isle and Camas Nathais. Greater dominance was exhibited by its more abundant species, but the distribution of individuals amongst the rarer species was more even. The curve for the Loch Creran site indicated that its community had the greatest overall dominance and hence least diversity.

Investigation of polychaete feeding categories was based on the feeding biology criteria proposed by Fauchald & Jumars (1979). These are, polychaete feeding mode, feeding motility and feeding morphology. For this study, feeding mode included 5 components, motility, 3 components and functional feeding morphology, 3 components.

Figure 2.4 K-Dominance plots of the communities from the four sample sites, Loch Creran, Loch Riddon, Camas Nathais and Creag Isle.



Feeding Mode	1.	Sub-surface deposit feeder (B)
	2.	Surface deposit feeder (S)
	3.	Suspension feeder (F)
	4.	Carnivore (C)
	5.	Omnivore/scavenger (V)
Motility	1.	Motile (M)
	2.	Discretely motile (D)
	3.	Sessile (L)
Morphology	1.	Jawed (J)
	2.	Tentaculate (T)
	3.	Soft proboscis (X)

Discretely motile refers to an organism that is capable of moving from place to place, but is sessile whilst feeding. This scheme follows that of Fauchald & Jumars (1979) with the addition of the omnivore/scavenger component and the absence of their herbivore component, which was not represented in this study.

The percentage composition of these categories for each site is shown in Fig. 2.5. Table 2.5 shows these observed percentage compositions in a contingency table, testing the association between sites and feeding category (Chi-squared test). As part of this test, expected values of percentage composition were calculated and compared against the observed percentages. This was assuming the null hypothesis that the proportion of each type of polychaete (for each of the three feeding categories), was the same at each of the four sites. A highly significant association ($P < 0.001$) was demonstrated between site and the components of each of the three feeding groups. At the Loch Creran site, a higher than expected proportion of surface deposit feeders

Figure 2.5 Percentage composition of polychaete individuals in feeding, motility and morphology categories for each of the sample sites. Different components are identified in the adjoining text.

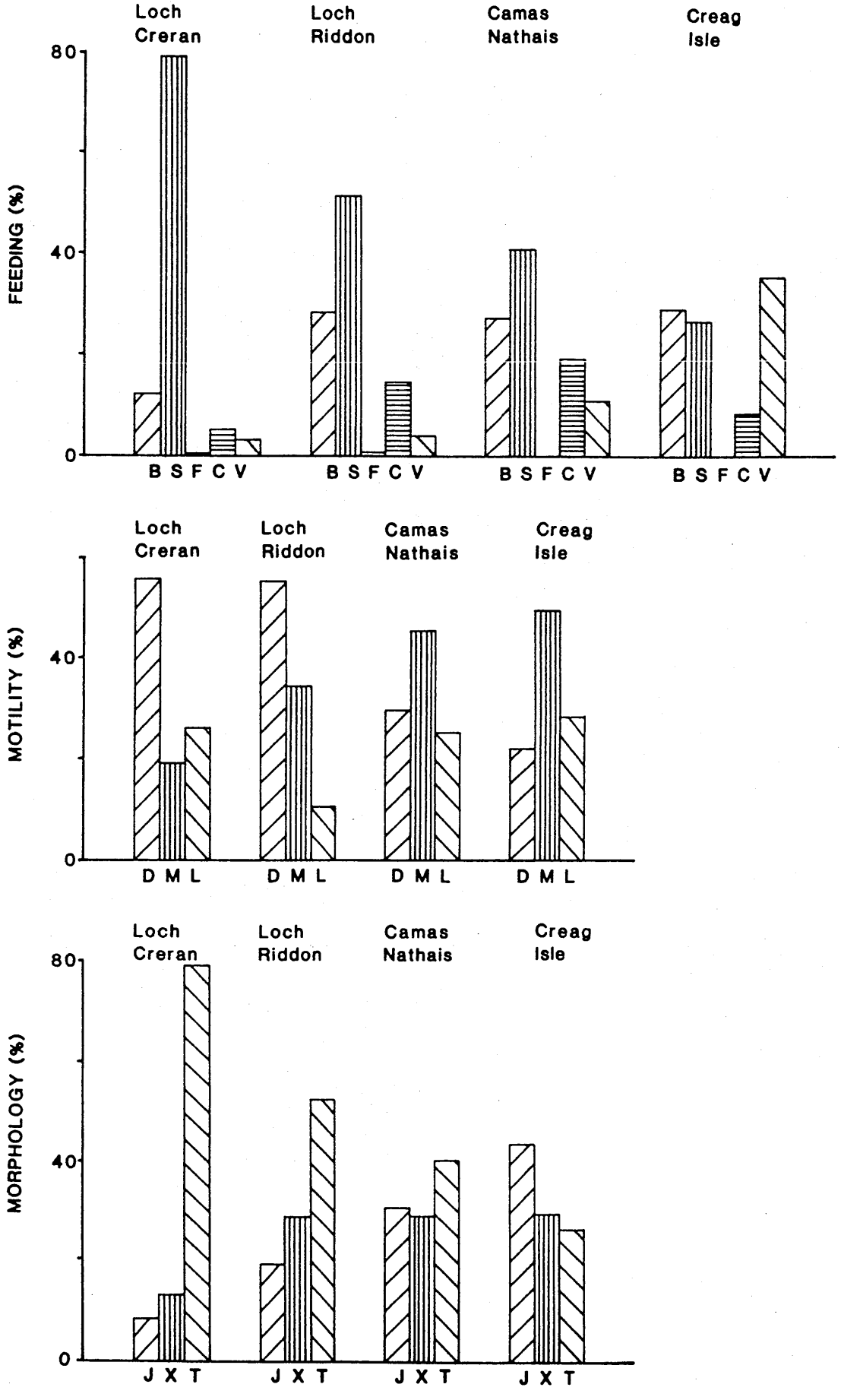


Table 2.5 Observed and Expected (χ^2-test) percentage compositions of polychaete individuals in feeding, motility and morphology categories for each of the sample sites. Different components are identified in the adjoining text.

	LOCH CRERAN		LOCH RIDDON		CAMAS NATHAIS		CREAG ISLE	
Component	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
1. Feeding								
B	12.2	24.4	28.6	24.4	27.7	24.4	29.0	24.4
S	79.2*	49.7	51.6	49.7	41.2	49.7	26.9*	49.7
C	5.0	11.8	14.8	11.8	19.3	11.8	8.3	11.8
V	3.5	13.9	4.8	13.9	11.8	13.9	35.8*	13.9
2. Motility								
D	55.3*	40.5	55.1*	40.5	29.7*	40.5	22.1*	40.5
M	18.9*	37.0	34.0	37.0	45.2	37.0	49.6*	37.0
L	25.8	22.4	10.4*	22.4	25.1	22.4	28.3	22.4
3. Morphology								
J	8.1*	25.3	18.9	25.3	30.8	25.3	43.4*	25.3
X	13.1	25.1	28.7	25.1	29.1	25.1	29.6	25.1
T	78.8*	49.5	52.4	49.5	40.1	49.5	26.9*	49.5

* More than 10% difference between observed and expected values.

A highly significant association was shown between the sites and each of the three feeding categories ($P < 0.001$).

was recorded (in Table 2.5, if the observed proportion of any component differed more than 10% from the expected proportion, that result was highlighted with an asterisk). This was mainly due to the high abundances of A. tullbergi and M. palmata. The proportion of sub-surface deposit feeders was lower than expected at the Creag Isle site, whilst the proportion of omnivore/scavengers was higher (largely comprised of Nephtys hombergii).

Within the feeding motility category, there was a higher than expected proportion of discretely motile individuals at the Loch Creran and Loch Riddon sites (again due to the species previously noted). However, at the Creag Isle site, motile individuals were dominant and were higher in number than expected (Lumbrineris hibernica and N. hombergii). A lower than expected proportion of sessile individuals were recorded at the Loch Riddon site.

Within the feeding morphology category, tentaculate individuals were the overriding dominants at the Loch Creran site (78.8%). Jawed individuals occurred in higher than expected proportions at the Creag Isle site. In each of these cases, the high numbers of the same above-mentioned species were again largely responsible.

2.4.2 Sediment Analysis

The data from the granulometric analysis of each site were presented graphically as a cumulative dry weight plot on a probability scale in Figure 2.6. All curves exhibited a basic sigmoid shape with an increasing percentage of fine material. The major sedimentary parameters are shown in Table 2.6. This shows the percentage composition of the sediments in terms of sand, silt and clay, organic content and median grain size (in phi units and microns). There was a highly significant difference ($P < 0.001$) in the distribution of grain sizes at the different sites as shown in Figure 2.7. However, the distributions of the Loch Creran, Loch Riddon and Creag Isle sites were similar in terms of median grain size (6-7 μm), while the sediments

Figure 2.6 Sediment composition for each of the sample sites.

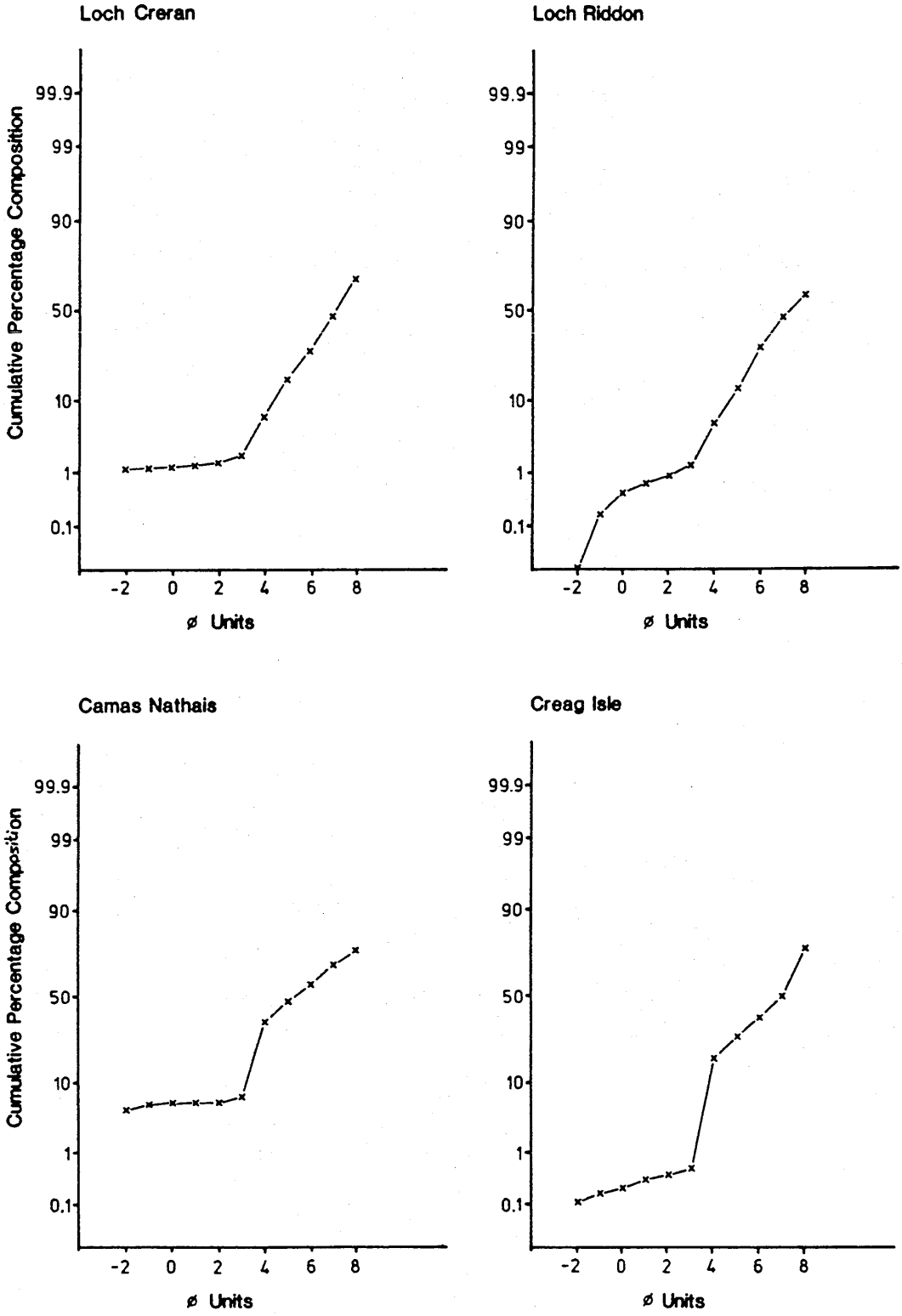
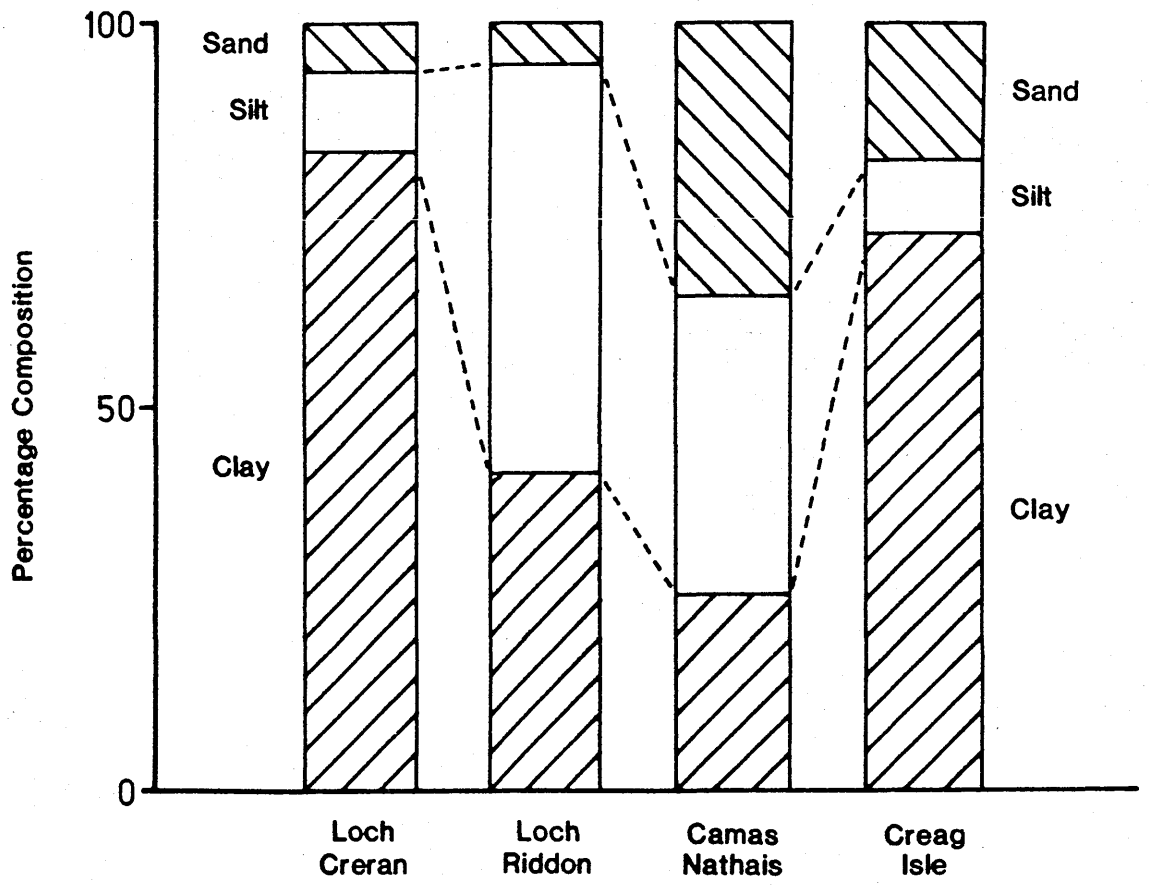


Table 2.6 Sedimentary parameters for each of the sample sites, including percentage composition of sand, silt and clay, organic content, median grain size in phi units (Mdϕ) and microns (Mdμ), degree of skewness and degree of sorting.

	Loch Creran	Loch Riddon	Camas Nathais	Creag Isle
Sand (%)	6.18	5.20	35.59	17.89
Silt (%)	10.47	53.59	38.28	9.63
Clay (%)	83.35	41.21	26.12	72.48
Organic (%)	3.37	1.35	0.99	1.14
Mdϕ	7.2	7.3	5.4	7.0
Mdμ	6.80	6.34	23.68	7.81
Strongly fine skew	*	*		*
Fine skew			*	
Poorly sorted	*	*	*	*

Figure 2.7 Sedimentary composition for each of the sample sites.



from the Camas Nathais site were much coarser (24 μm). In terms of combined silt-clay, the two sea lochs were quite similar (approximately 94%), although the proportions of the two sedimentary components differed. The Loch Creran site had the greatest proportion of clay (83%), with a similar high proportion at the Creag Isle site. Camas Nathais had the highest proportion of sand (35.6%) and lowest proportion of clay. All sediments were poorly sorted and exhibited a degree of positive skewness.

The level of organic content was highest at the Loch Creran site (3.4%) and lowest at the Camas Nathais site (0.99%). Loch Riddon and Creag Isle had intermediate low levels of 1.35% and 1.14% respectively.

2.4.3 Megafaunal Community Structure

Of the megafaunal burrowing crustaceans, two species could accurately be associated with their particular characteristic burrows. These were N. norvegicus and C. macandreae. Sedimentary mounds were present at some of the sites, which have previously been associated with Callianassa subterranea (Atkinson & Nash, 1985). However, from the resin casts, two species were found to be associated with these mounds, C. subterranea and an unidentified burrower which is subsequently referred to as Species X.

Data from the megafaunal transects is shown in Table 2.7. Each column represents the density per square metre of each particular feature for each site. The last row represents the total area surveyed at each site. As well as burrow structures, large surface-visible infaunal species were also noted. These were the pennatulids Virgularia mirabilis, Pennatula phosphorea and Funiculina quadrangularis, the anemone Cerianthus lloydii and large individuals (siphon diameter greater than 1.0 cm) of the bivalve Mya truncata. This last species was recorded by observation only at the Camas Nathais site, although small individuals were noted in the macrofaunal samples from all but the Creag Isle site (Table 2.1).

Table2.7 Abundance (per m^2) of megafaunal features/species at the different sample sites with areas surveyed.

	Loch Creran	Loch Riddon	Camas Nathais	Creag Isle
Total Burrow Openings	3.85	3.50	2.46	11.08
Total burrow Systems	1.83	0.97	1.28	5.40
Burrows of Nephrops norvegicus	0.11	0.76	0.02	0.35
Burrows of Calocaris macandreae	0.57	1.00	1.58	7.22
Large Callianassid-type Mounds	1.26	0.05	-	0.75
Burrows of Lesueurigobius friesii	0.25	0.11	0.14	0.20
Other Burrows	0.41	0.32	0.50	1.10
Virgularia mirabilis	4.11	0.13	*	-
Pennatula phosphorea	-	-	0.5	8.4
Funiculina quadrangularis	-	-	-	0.1
Cerianthus lloydii	0.54	-	0.12	0.35
Mya truncata	-	-	0.5	-
Area Surveyed (M^2)	46	38	50	20

* Very high densities, not recorded.

Of the pennatulids, F. quadrangularis was only observed at the Creag Isle site. Individuals observed reached over 40 cm above the sediment surface, but were very widely spaced. P. phosphorea occurred in high densities at this site ($8.4m^{-2}$) but only occurred in low densities at the adjacent Camas Nathais site. V. mirabilis was not observed at Creag Isle. Individuals were absent from the Loch Creran site and only present in low abundance at Loch Riddon. At Camas Nathais, they were so dense and in some cases so small that they could not be enumerated. An abundance of 214 m^{-2} was recorded from the macrofaunal samples from this area (Table 2.2).

The total number of burrow openings was approximately 3 m^{-2} at the Loch Creran, Loch Riddon and Camas Nathais sites. At the Creag Isle site, however, openings were far more abundant (11 m^{-2}). Total burrow systems were defined as all the complexes of 2 or more openings. Again this was far higher at the Creag Isle site than at any of the others.

Of the identifiable burrow systems, Nephrops norvegicus burrows were dominant at the Loch Riddon site (0.76 m^{-2}), Calocaris macandreae burrows at the Creag Isle site (7.22 m^{-2}) and callianassid-type mounds at the Loch Creran site (1.26 m^{-2}). Goby burrows (mostly Lesueurigobius friesii) occurred at all the sites in densities of 0.1 to 0.25 m^{-2}. Other burrows included burrow openings that could not be assigned to one of the above. Most were of the form of a simple tapering funnel entrance similar to that of C. macandreae but connecting to a much finer system. It was thought that these may be due to other macrofaunal species such as polychaetes or holothurians.

Representative casts of N. norvegicus, C. macandreae, C. subterranea and Species X were analysed. Basic measurements made from the resin casts are shown in Table 2.8. Columns referred to are: number of shafts - the number of openings up to the sediment surface from the burrow complex with the number of blocked or unfinished shafts in brackets. Volume referred to the burrow lumen volume in ml. Surface area of the cast refers to the total

Table 2.8 Numerical data obtained from analysis of resin casts.

Species	Cast No.	Shafts *	Vol. (ml)	Surface Area (cm^2)	Area covered (cm^2)	Shaft Diam. (cm)	Tunnel Height (cm)	Tunnel Width (cm)	Max. Depth (cm)	Major Horizons (cm)
Nephrops norvegicus	CI.1	2	1702	2071	0.302	-	2.8	3.6	26.7	16
"	CI.5	1	1240	876	0.096	-	2.65	5.2	21.5	12
"	CN.1	7	3359	3027	0.503	-	1.85	2.05	13.4	12
"	Cr.11	1	107	127	0.071	-	1.2	1.35	12.8	9
Calocaris macandreae	CI.2	7(5)	1076	1434	0.159	2.2	1.5	2.0	15.0	8, 10, 14
"	CI.3	8(1)	612	1195	0.077	1.5	1.5	1.7	15.8	8, 11, 14
"	CI.4	9	909	1514	0.171	1.7	1.7	2.3	17	7, 9, 12
"	CI.6	6(8)	413	1036	0.109	1.9	1.65	1.8	12	3, 7, 9, 12
"	CI.7	5	479	1115	0.131	1.55	1.75	1.95	12.7	6, 8, 12
Calocaris/ Callianassa	CI.8	3(2)	1124	2151	0.131	1.7/1.0	1.6/1.15	1.9/1.25	45	7, 9, 12/30, 43
"	CI.9	12(2)	1578	2868	0.086	1.5/1.1	1.4/1.0	1.5/1.0	36	7, 10, 15/30
Callianassa subterranea	CI.10	2	1174	1842	0.560	1.3	1.6	1.7	48	35
"	CI.11	1(2)	744	1434	0.141	1.0	1.0	1.0	62	52
"	CI.12	1	1281	1832	0.217	1.5	1.6	1.6	41	38
"	Cr.0	0(1)	339	1115	0.238	-	1.1	1.2	-	> 30
Species 'X'	Cr.1	1	413	717	0.050	0.85	2.1	2.5	44	-
"	Cr.2	1	612	1275	0.085	0.95	1.9	2.45	45	-
"	Cr.7	1	355	637	0.050	0.85	1.6	2.3	62	-
"	Cr.9	1	719	1020	0.061	0.95	2.2	2.55	54	-
"	Cr.12	1	215	391	0.038	0.7	1.2	1.85	51	-
"	Cr.13	1	256	669	0.034	1.0	1.75	1.9	48	-
"	Cr.17	1	380	690	0.034	0.75	1.75	2.5	30	-
"	Cr.19	1	248	398	0.023	1.0	2.05	2.55	47	-
"	Cr.21	1	380	558	0.039	0.9	1.9	2.55	45	-

* Collapsed or closed risers in brackets.

surface area of the resin (in cm^2). Area covered was an approximate measurement of the area of sediment surface under which the burrow lay, this was calculated by multiplying the maximum length by the horizontal width of the cast. Shaft diameter, tunnel height and tunnel width were all average measures taken from several measurements of each cast. Two figures were given for the joint C. macandreae/C. subterranea complexes, the first measurement referring to the former, the second to the latter. Maximum depth was given as the maximum vertical depth reached by the cast below the sediment surface. Major horizons were defined as the depths at which major galleries occurred in the casts. Average cast measurements for each species are shown in Table 2.9.

The largest casts recovered in terms of volume and surface area were those of N. norvegicus. A typical large complex is shown in Plate 2.1. Casts of this species consisted of simple linked tunnels of sub-circular cross section sloping up to the wide tunnel openings. Maximum depth was approximately 20 cm going deeper with larger casts.

The casts of C. macandreae were multi-galleried shallow burrows (gallery refers to a "tunnel ..... or dominantly horizontal component of a burrow system having prominent vertical and horizontal parts" as defined by Frey, 1973). Two typical casts are shown in Plate 2.2. Shafts were circular in cross section with increasing diameter just below the sediment surface. Tunnels were many branching, of sub-circular cross section with multi-gallery horizons occurring between 3 and 15 cm depth. One cast contained a recognizable circular gallery visible in the underneath view of cast C.I.7 in Plate 2.2.

Two casts were recovered which contained galleries characteristic of both C. macandreae and C. subterranea, connected but with individual gallery systems. These are shown in Plates 2.3 and 2.4. When casting the diver assumed that the burrow belonged to C. macandreae alone as no characteristic

Table 2.9 Average cast dimensions of the four dominant megafaunal species.

Spp.	Shafts No.	Vol. (ml)	Surface Area (cm^2)	Area Covered (cm^2)	Shaft Diam. (cm)	Tunnel Height (cm)	Tunnel Width (cm)	Max. Depth (cm)
Nephrops norvegicus	2.75	1602	1525	0.243	-	2.13	3.05	18.6
Calocaris macandreae	7.2	698	1259	0.129	1.77	1.62	1.95	14.5
Callianassa subterranea	1	884	1556	0.289	1.27	1.33	1.38	50
Species X	1	398	706	0.046	0.88	1.61	2.35	47.3

Plate 2.1 Resin cast of the burrow of Nephrops norvegicus from Camas Nathais

(a) Side view of cast CN1

(b) Ventral view of cast CN1

Scale bars show 1 cm divisions


a

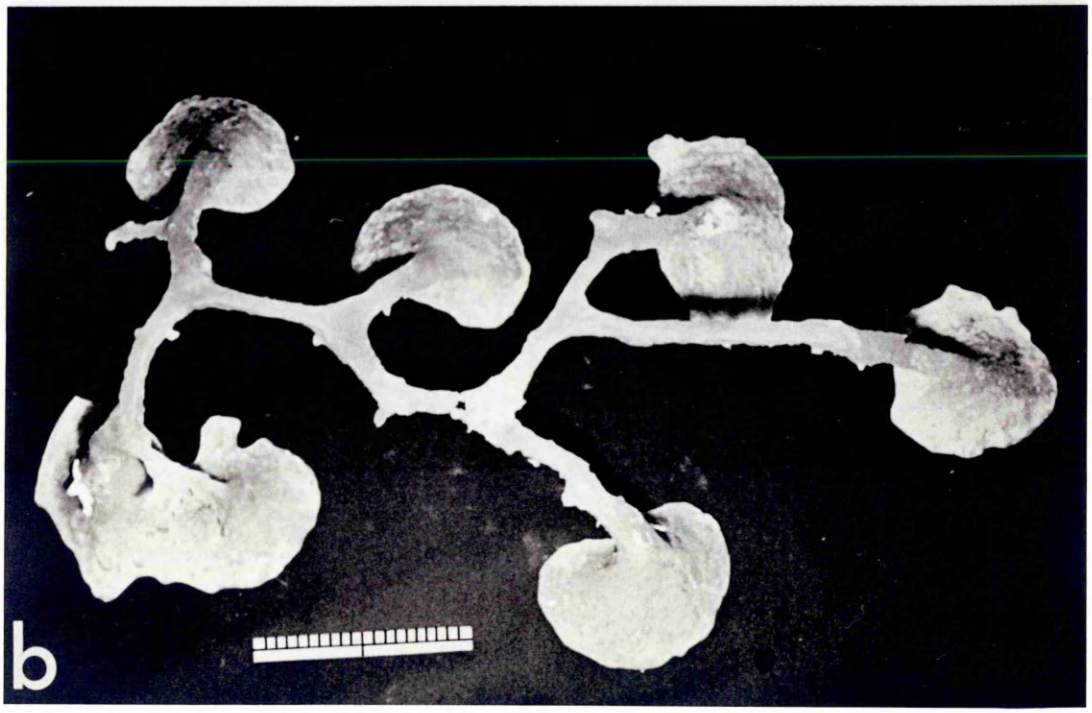

b

Plate 2.2. Resin casts of the burrows of Calocaris macandreae from Creag Isle

(a) Side view of cast C.I.7

(b) Ventral view of cast C.I.7

(c) Ventral view of cast C.I.6

(d) Side view of cast C.I.6

Scale bars show 1 cm divisions

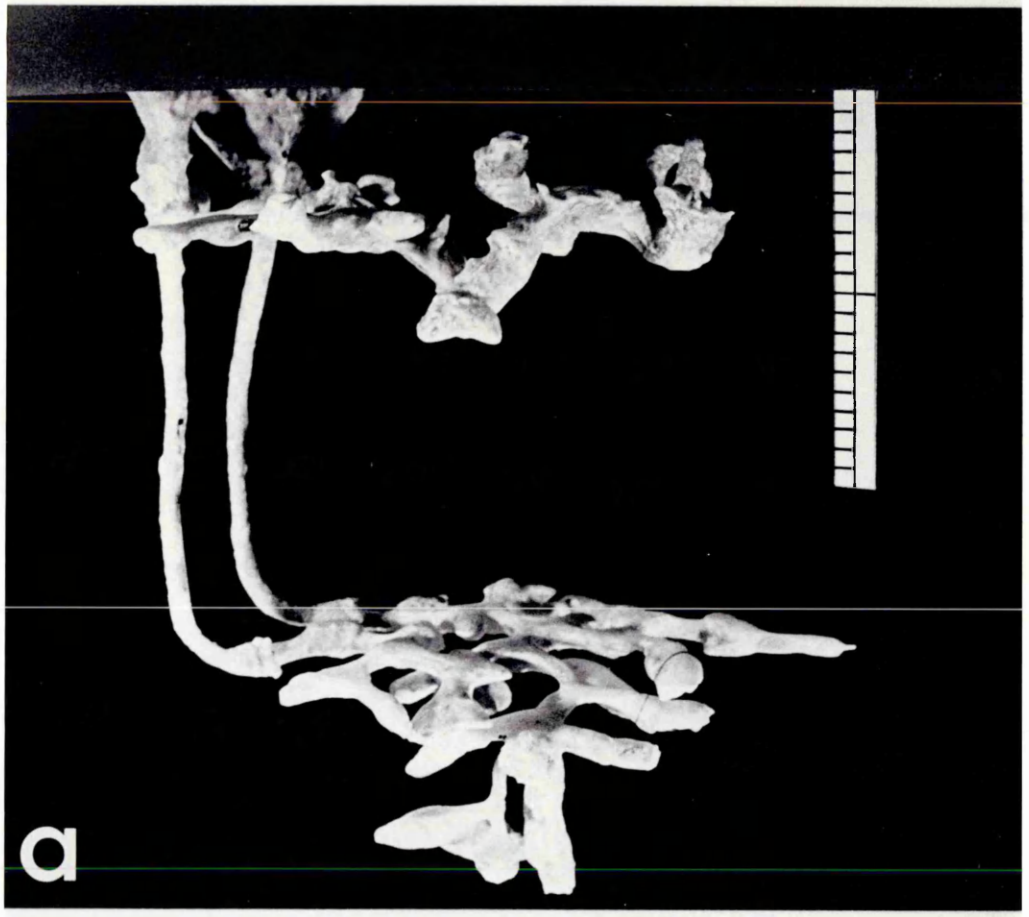
a
b
c
d

Plate 2.3 Resin cast of a burrow complex containing components of both Calocaris macandreae (upper gallery system) and Callianassa subterranea (lower gallery system) from Creag Isle

(a) Side view of cast C.I.8

(b) Ventral view of cast C.I.8

Scale bars show 1 cm divisions


a

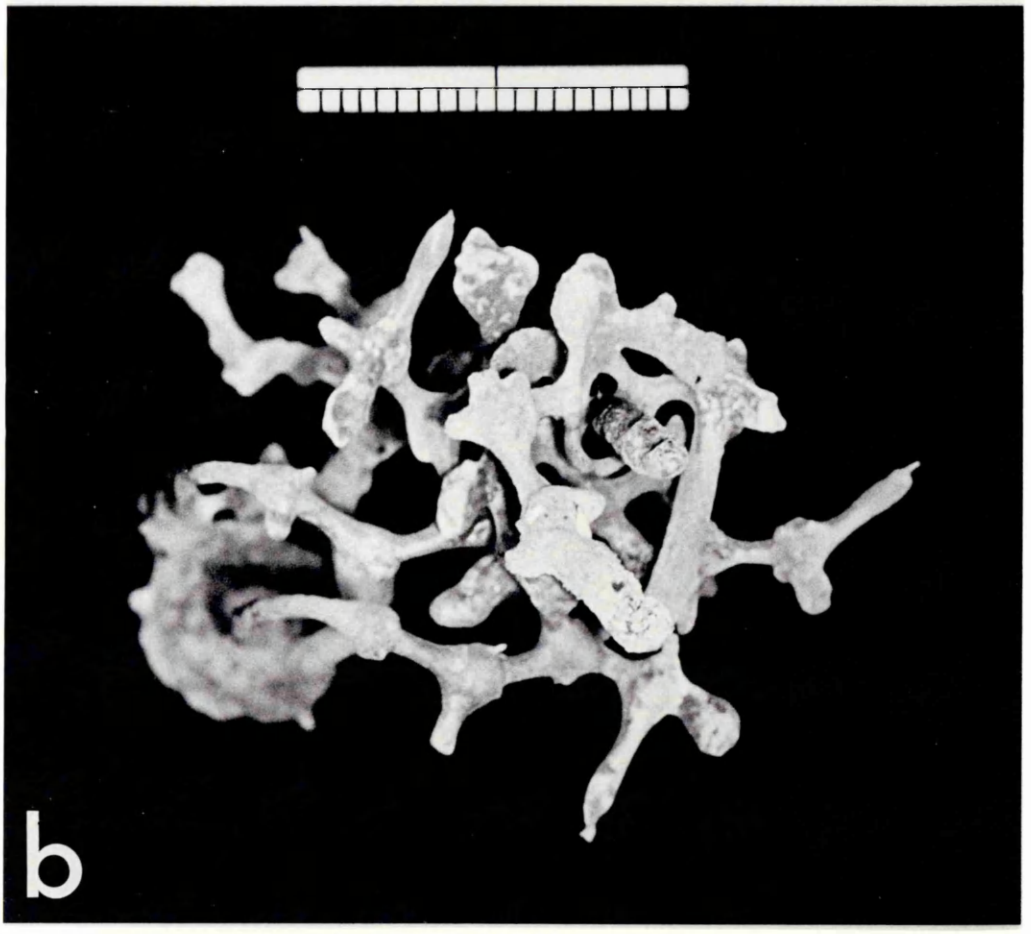
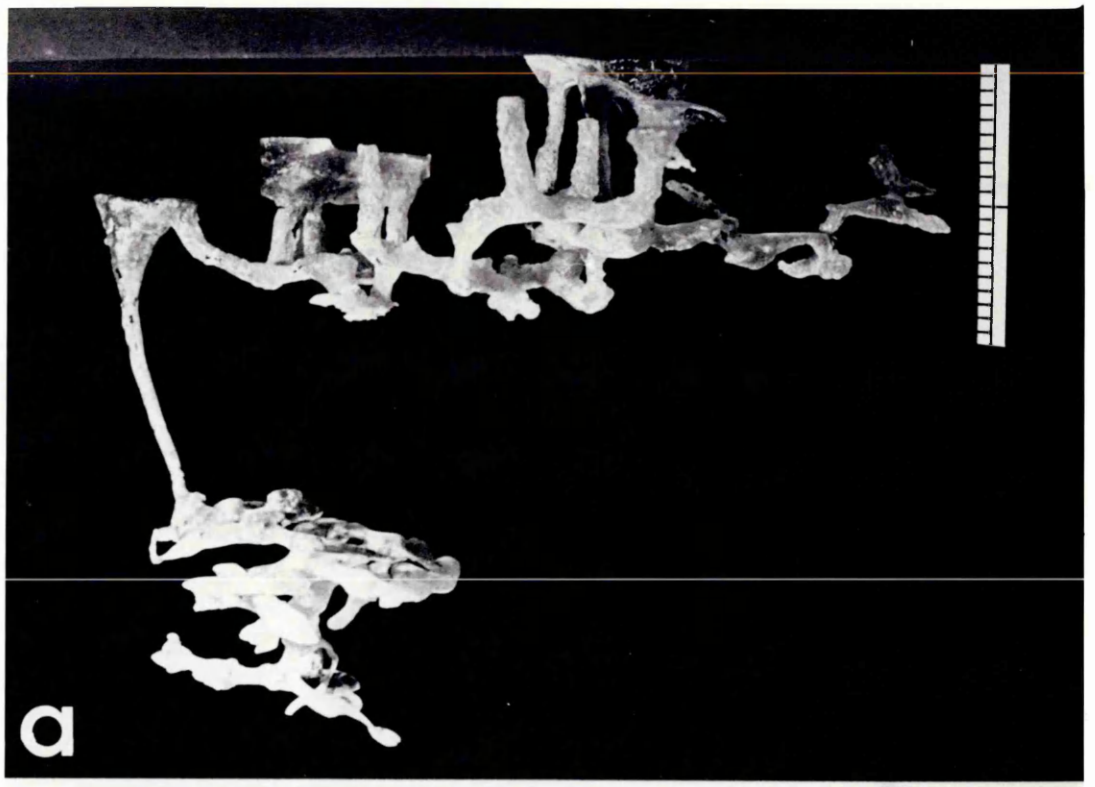
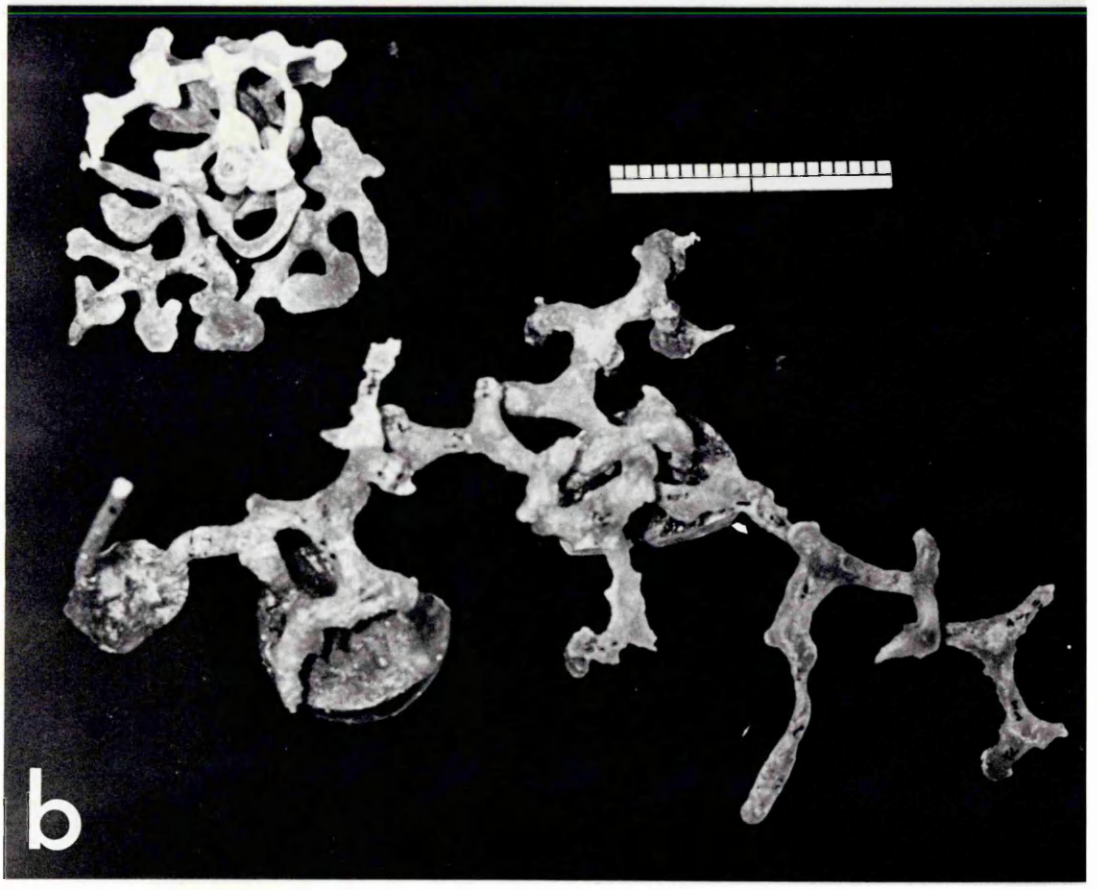

b

Plate 2.4 Resin cast of a burrow complex containing components of both Calocaris macandreae (upper gallery system) and Callianassa subterranea (lower gallery system) from Creag Isle

(a) Side view of cast C.I.9

(b) Ventral view of cast C.I.9 with lower gallery system offset


a


b

mounds of C. subterranea were visible. These joint burrows were extensive, having large volumes and surface areas.

The C. subterranea casts consisted of a long narrow riser with a complex nodular (lattice-like) gallery system between 30 and 60 cm depth. One very elongate cast (CI10) with side connecting tunnels is shown in Plate 2.5, whilst a more typical cast is shown in Plate 2.6. Risers were circular in cross section and approximately 1.0 cm in diameter. Nodes were often tripartite or quadripartite. Galleries ended in nodes that were vaguely snake-head in shape, approximately 2.5-3.0 cm wide and 1.5-2.0 cm high.

The casts of species X were simple curved L-shaped tunnels without a lattice-like system. Two typical casts are shown in Plate 2.7 (Cr7 and Cr2). The horizontal tunnel and vertical shaft varied in diameter and shape, occasionally spiralling down. The entrance to the system was a funnel on top of a C. subterranea-type mound. Below the funnel was a constriction of less than 1.0 cm diameter extending down for approximately 10 cm. This shaft widened below this and levelled out to the horizontal. At this point the tunnel was more elliptical in cross section, approximately 2.3 cm wide and 1.6 cm high. The roof of the tunnel had semi-circular striations across the top. Maximum depth at this section was approximately 47 cm.

The average measurements taken from the casts (Table 2.9) were combined with the megafaunal abundance data in Table 2.7 to give approximate values as to the increase in surface area and sediment water content due to megafaunal presence at each site. To arrive at the values in Table 2.10, average volume and surface area per burrow opening were calculated for each species. Average number of openings per burrow type were calculated from the raw data of the transects (not shown). The two sets of figures were multiplied to give the data in Table 2.10. As all the mounds cast in Loch Creran proved to be Species X, only the data for that species were used for that site. Data for C. subterranea were used for the mounds

Plate 2.5 Resin cast of an extended burrow of Callianassa subterranea from Creag Isle

(a) Side view of cast C.I.10

(b) Ventral view of cast C.I.10

Scale bars show 1 cm divisions

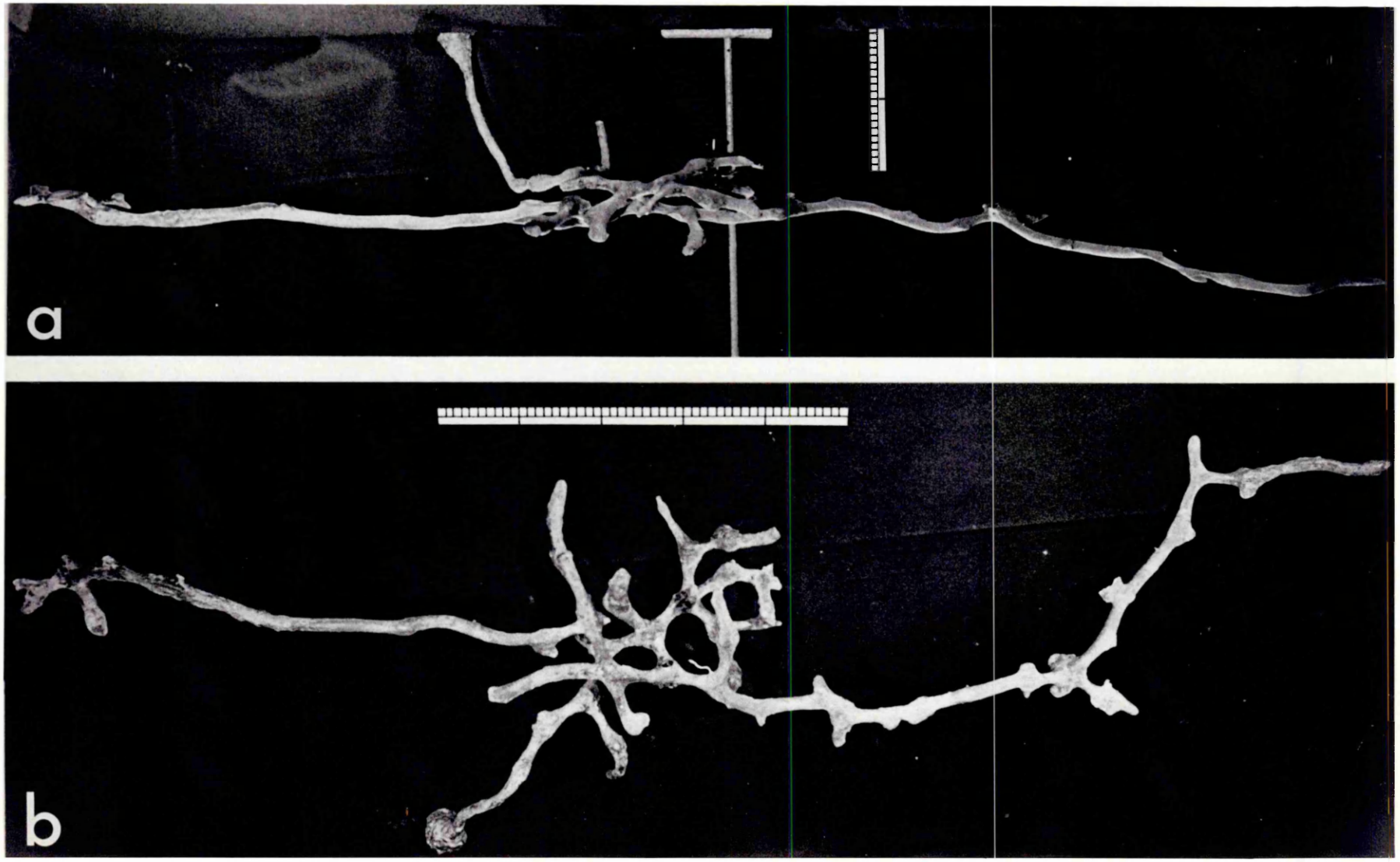
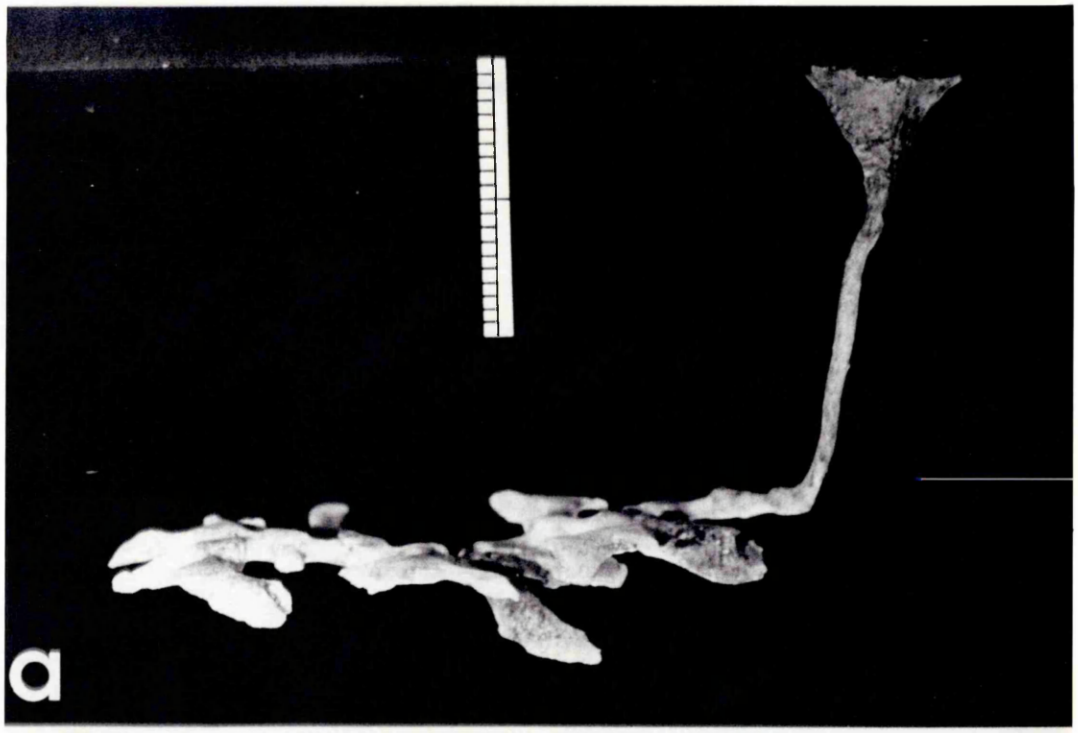

a
b

Plate 2.6 Resin cast of the burrow of Callianassa subterranea from Creag Isle

(a) Side view of cast C.I.12

(b) Ventral view of cast C.I.12

Scale bars show 1 cm divisions


a

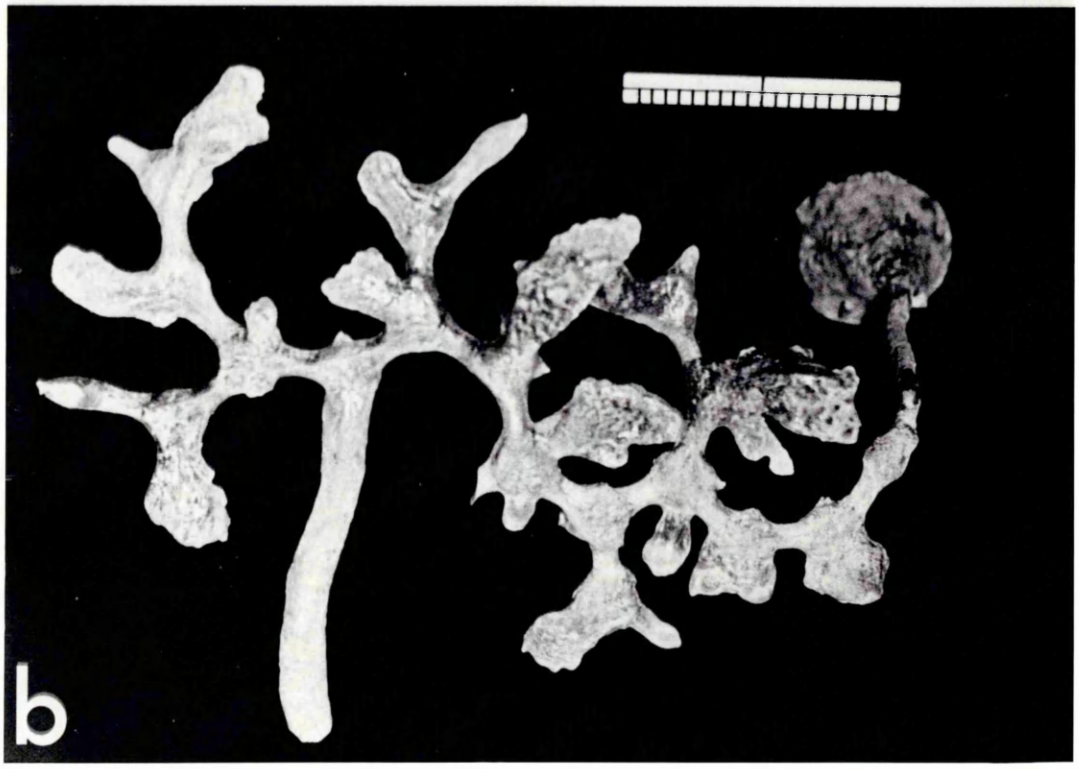

b

Plate 2.7 Resin casts of the burrows of Species X from Loch Creran

(a) Side view of cast Cr7

(b) Side view of cast Cr2

Scale bars show 1 cm divisions

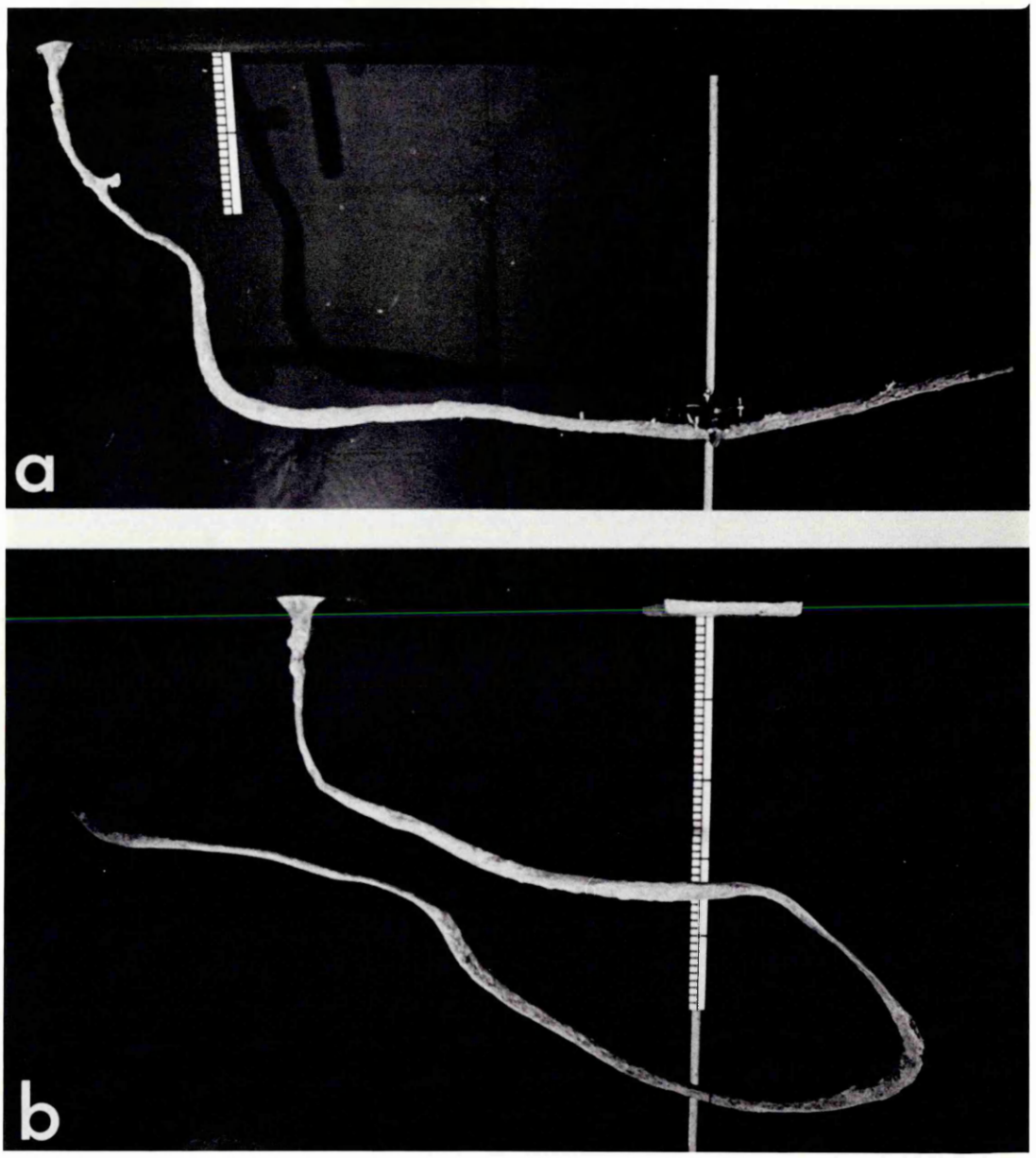

a
b

Table 2.10

Average increase in surface areas due to megafaunal burrow structures at each site (m^2).

	Loch Creran	Loch Riddon	Camas Nathais	Creag Isle
Nephrops norvegicus	0.026	0.180	0.005	0.080
Calocaris macandreae	0.011	0.019	0.030	0.136
Callianassa subterranea	-	0.004	-	0.055
Species X	0.05	-	-	-
Total Percentage Increase	8.7	23.9	3.5	27.1

Average increase in water content of sediment contained in megafaunal burrow lumens (ml/m^2) at each site.

	Loch Creran	Loch Riddon	Camas Nathais	Creag Isle
Nephrops norvegicus	237	1639	43	755
Calocaris macandreae	199	350	553	2527
Callianassa subterranea	-	66	-	994
Species X	890	-	-	-
Total	1326	2055	596	4276

observed at the other sites as no casts of Species X were recovered outside of Loch Creran. Considering just the four megafaunal species in Table 2.9, an increase in surface area of approximately 27% was calculated for the well burrowed site of Creag Isle, 24% for Loch Riddon, 8.7% for Loch Creran and 3.5% for Camas Nathais. Megafaunal burrow lumens contained an approximate volume of 4276 $ml m^{-2}$ of water at Creag Isle, with lesser volumes at the other sites.

Using the information drawn from this chapter on the dominant mega- and macrofaunal species at each sampling site, comparative schematic illustrations were drawn up to summarize the data. These are shown in Figure 2.8.

2.5 DISCUSSION

2.5.1 Site Characteristics

Although the four sites investigated were similar in terms of the presence of soft sediments, each site had different physical and hydrographic characteristics. The four sites were situated in firths, the Firth of Clyde and the Firth of Lorne. These partially enclosed bodies of water are, by nature, fjordic (Edwards et al., 1986). Two of the sites, Camas Nathais and Creag Isle, were situated in the more open part of the Firth of Lorne (Lynne of Lorne). The other two sites were situated in inner sea lochs which are classified as fjords (semi-enclosed elongated basins connected to more open water by shallow narrow sills -for a full definition, see Syvitski et al., 1987).

These shallow sea lochs are potentially areas of high productivity owing to semi-confinement, nutrient input from fresh-water run-off, high fluvial carbon input and well linked benthic-pelagic coupling, leading to rapid recycling of carbon and nutrients. Chlorophyll biomasses measured in August 1980 by Grantham (1981) at the sampling site in Loch Creran were twice as

Figure 2.8 Pictorial representation of the principal megafaunal burrow structures at each of the sample sites and the distribution of dominant macrofaunal species around these structures.

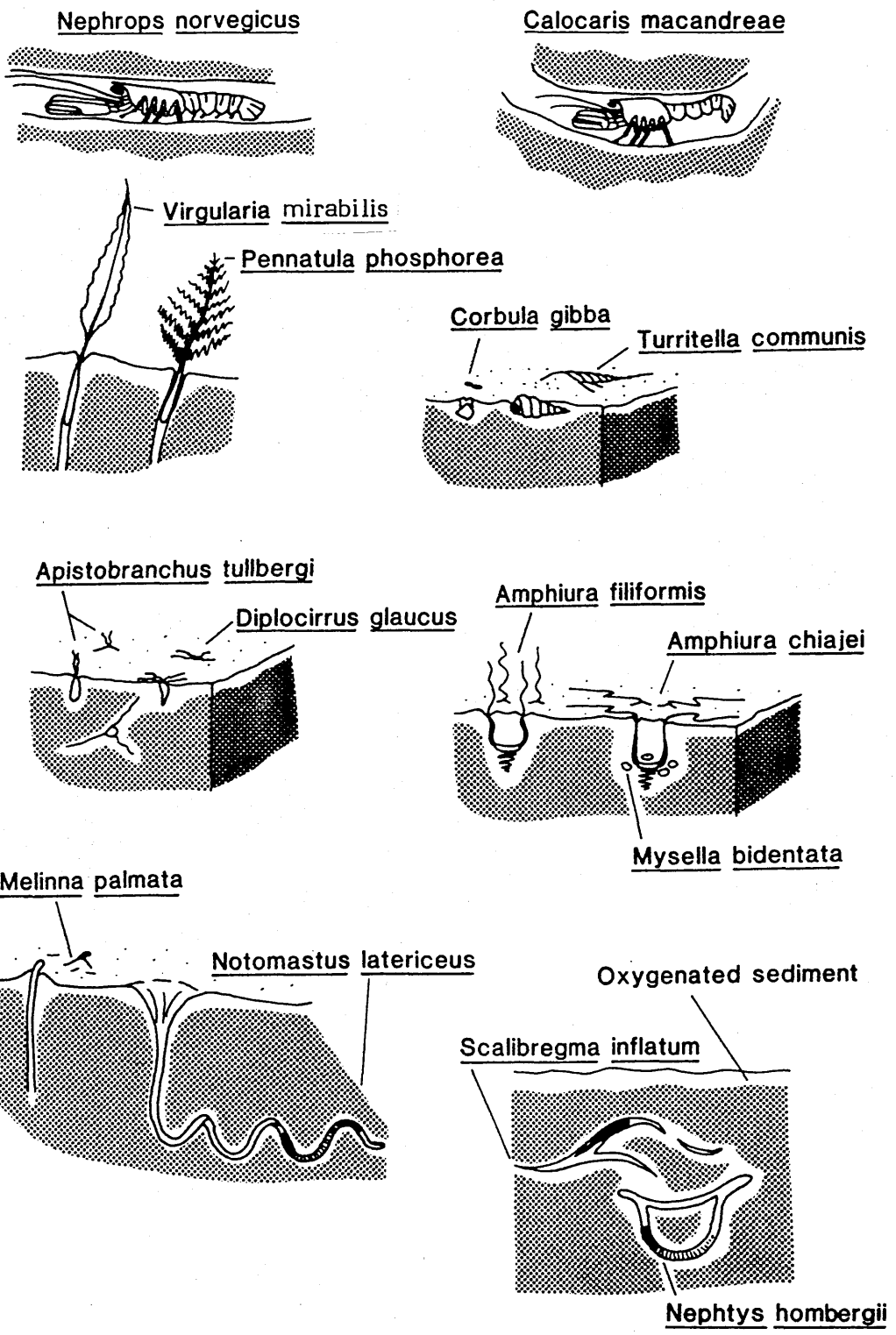


Figure 2.8 contd.

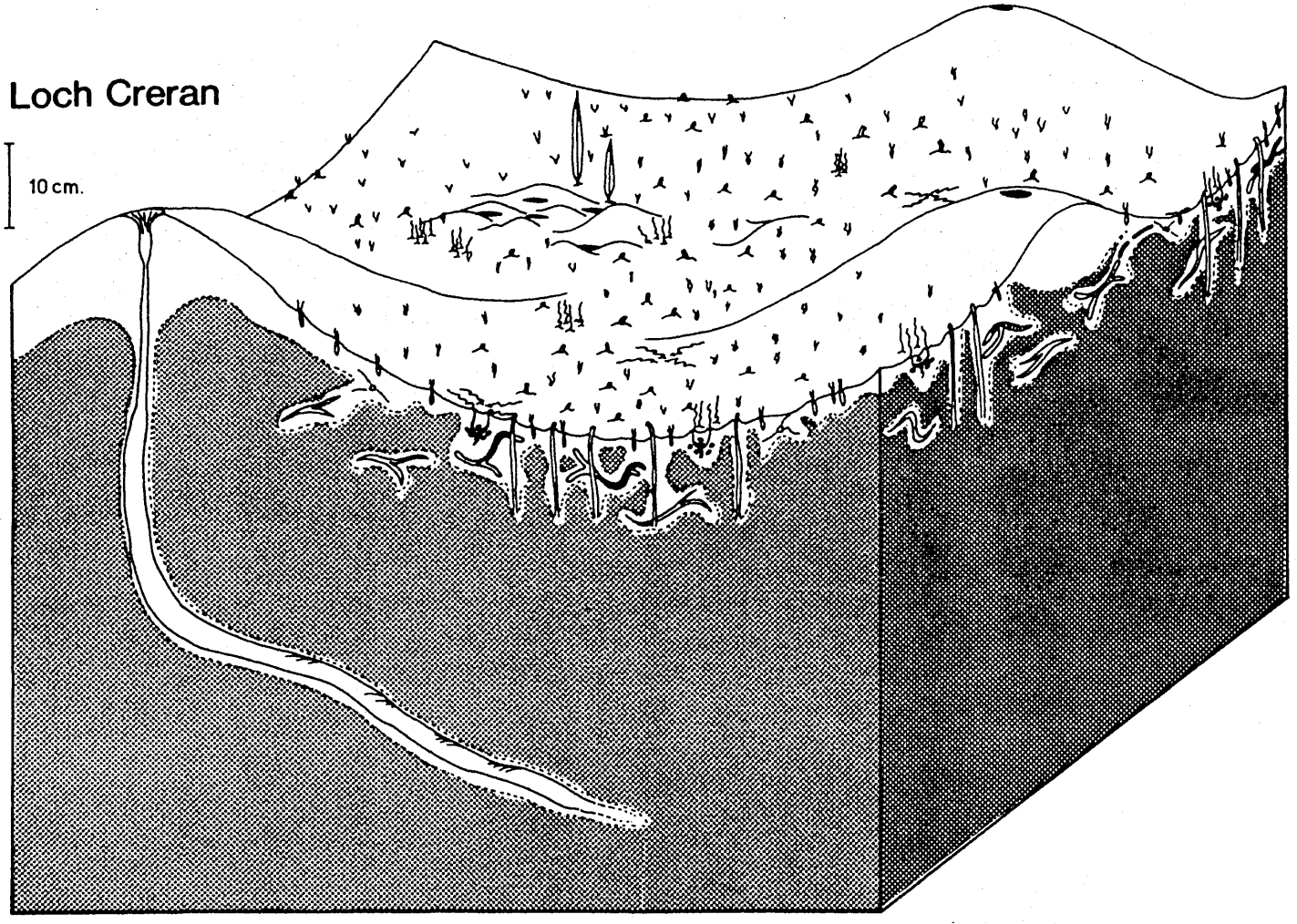


Figure 2.8 contd.

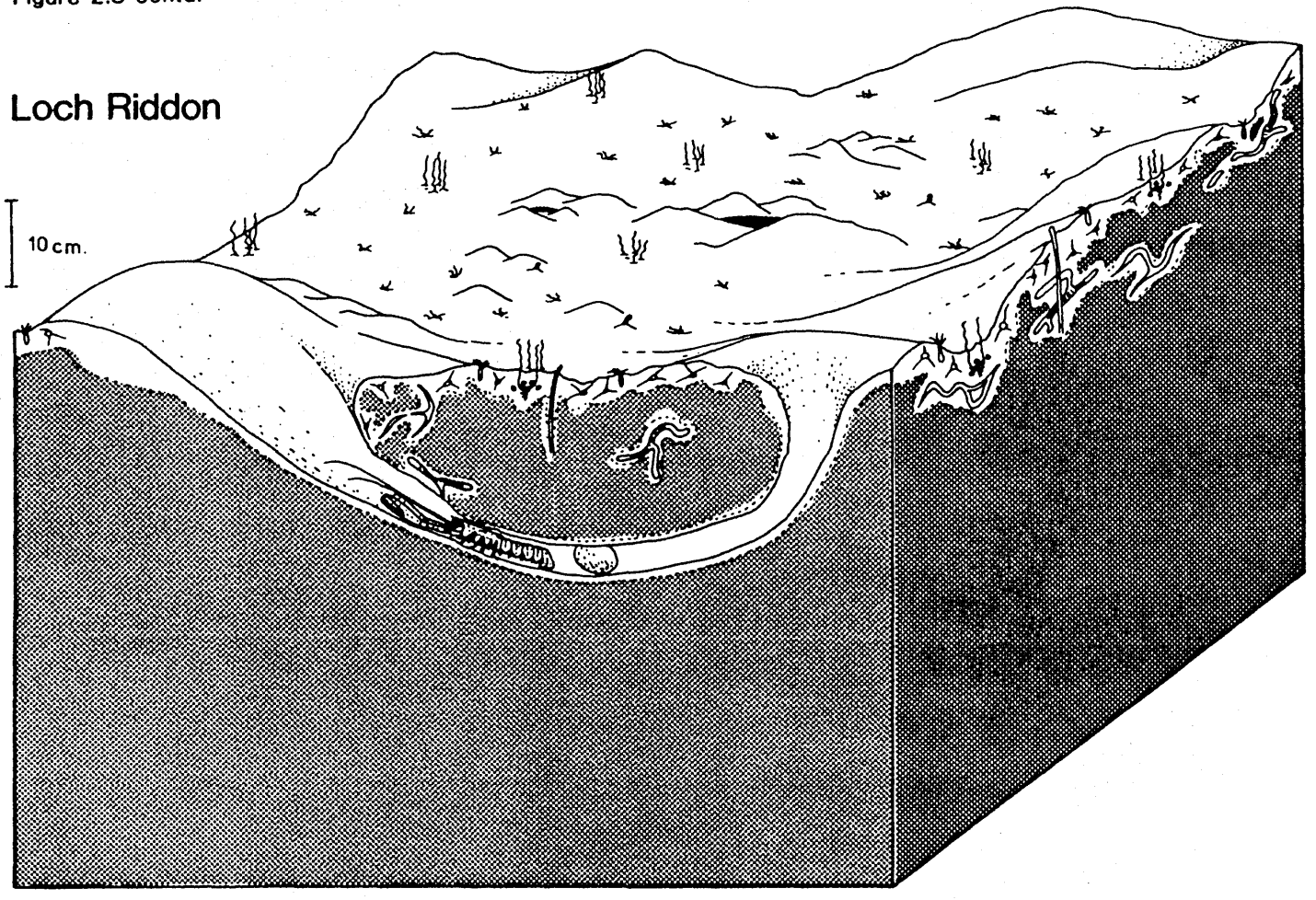


Figure 2.8 contd.

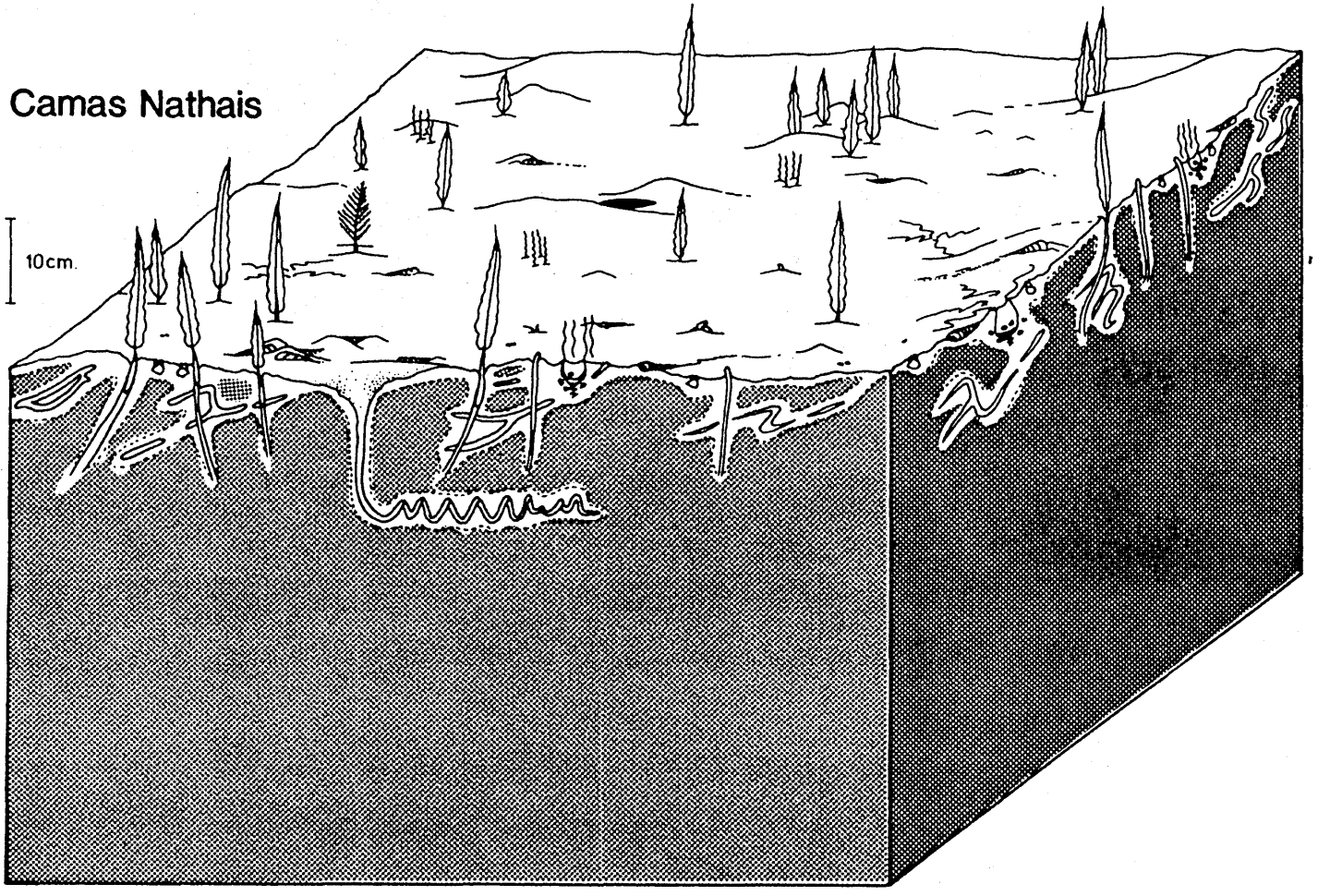
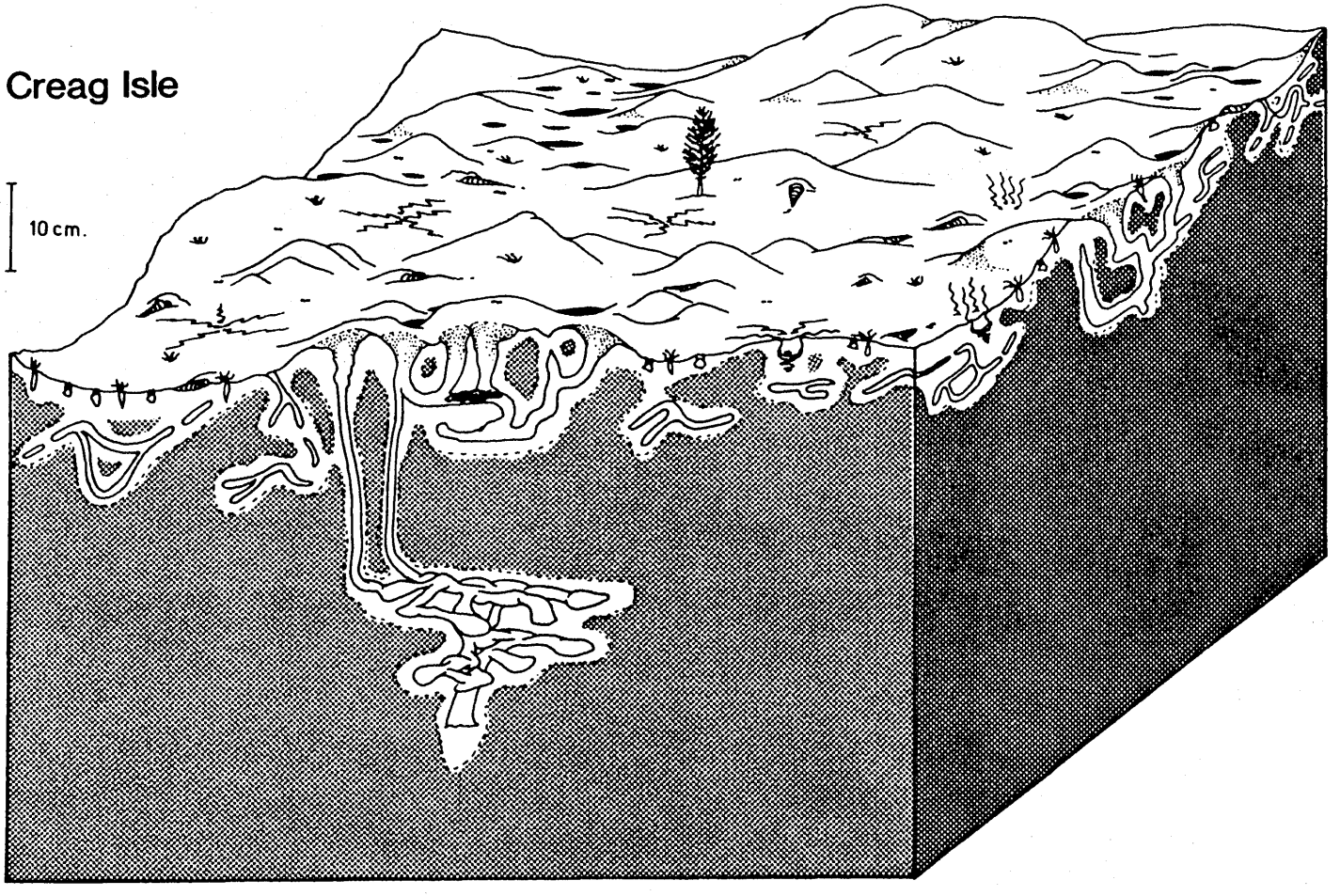


Figure 2.8 contd.



high as those at LY1, a few kilometres from both the Camas Nathais and Creag Isle sites. No measurements have been made in Loch Riddon, but Tett et al. (1986) have recorded measurements in the adjacent Loch Striven. This is a separate loch, but it was thought that it may have a similar standing crop to Loch Riddon. Tett et al. noted that median chlorophyll concentrations in Loch Striven were not significantly different from those of Loch Creran. They observed that the high standing crop of Loch Striven was aided by the eutrophic conditions in the Clyde, by nutrient rich water entering from the seaward end of the loch. Tett (1986) showed theoretically that there was relatively little net export of primary production from Loch Creran. Much of the primary production must therefore be available to secondary producers. This may be explained by the relatively good mixing processes compared to some other fjordic sea lochs. If on the other hand the water column were stratified, phytoplankton biomass would be mostly confined to the upper layers, which may be flushed directly from the loch.

In the Lynn of Lorne area standing crop, as noted above, was not as high as in the sea lochs. Decreased stratification away from the head of the Firth (Edwards et al., 1986), would lead to a greater degree of benthic-pelagic coupling and thus more efficient nutrient cycling. However, carbon and nutrients may be generally more limited in this area due to the lack of the inputs more characteristic of the lochs. Therefore, less production must be available to the secondary producers in this area.

In Loch Creran there is additional loading on the ecosystem from an alginate factory effluent. The annual discharge from this effluent in 1980 was reported to contain 2500 tonnes of particulate and 750 tonnes of dissolved organic carbon (Tyler, 1983). This was compared to annual phytoplankton input to the loch of 2565 tonnes. Much of the particulate matter settles in an unconsolidated heap around the effluent. The effects of this overlying material on the benthos were confined to an area of roughly 500 m^2 extending

in a plume some 200-300 m from the end of the effluent (Pearson & Stanley, 1977). The exact fate of the dissolved organic fraction is unknown, although any effects must be widespread. From observations of a pulpmill waste in Loch Eil, Pearson (1982) reported that sediment respiration rate increased with increased sediment loading of waste. It was concluded that there was no overall long term accumulation of organic carbon in the Loch Eil sediments. If this was also the case in Loch Creran, it could be assumed that nearly all the carbon input from the alginate effluent is mobilised into the loch ecosystem. This source, combined with the high phytoplankton biomass, would seem to make the loch system hypertrophic.

Within fjordic basins, there is a significant relationship between the distribution of sedimentary particles and water movement (Pearson, 1980). Reduction of water movement away from the head and turbulent sill areas results in an increase in the percentage of fine sediments (Syvitski et al., 1987). The high silt/clay content of sediments from the Loch Creran and Loch Riddon sites were typical of such basins (although this latter site may be more heterogeneous - see Section 2.2.1). The sediments of the Creag Isle site also showed a high silt/clay content. It was assumed that this area was one of low water movement. As described in Section 2.2.4, this site was situated in a soft sedimentary area surrounded by a deeper area of a more mixed sedimentary nature. It is possible that local water movement moves around this relatively shallower area allowing deposition of fine material. The sediments of the Camas Nathais site had a higher proportion of sand indicative of higher current velocities. Prevailing south-westerly winds may funnel waves straight into the bay causing a high degree of turbulent mixing. Further into the bay, sediments are predominately of a sandy nature.

Comparison of organic carbon content of the sediments with literature values can only be made with care owing to differing methods of sample collection and analysis. Mook & Hoskin (1982) have demonstrated much

variation and error by using the method of weight loss by ignition. They noted that sediments of high clay content could lose excess weight from loss of structural water.

As discussed, phytoplankton production may be high and well coupled to the benthos in the sea lochs. The sediments from the Loch Riddon and Loch Creran sites would therefore be expected to have high carbon contents. However, the sediment from the Loch Riddon site contained less than 1.5% carbon and it was felt that this result was somewhat anomalous. Previous analyses from this area have estimated the sedimentary carbon content to be 2-6% (Pearson et al., 1986a; pers. comm. R.J.A. Atkinson). This near shore area of the loch has been shown to be of a heterogeneous nature and the single sample may have been taken from a particular "uncharacteristic" patch. The sediment from the Loch Creran site had a carbon content of 3%, which was more typical of sea loch basins. Using an elemental analyser Pearson et al. (1982) found 2% organic carbon in the Loch Eil basin prior to the introduction of a pulp waste effluent (rising to 5% after introduction), and values of 3.5-4.5% were commonly found in the inner basin of a Shetland voe (Pearson & Eleftheriou, 1981). The organic contents from the Camas Nathais and Creag Isle sites were nearer to 1%, more typical of outer firth conditions.

2.5.2 Characteristics of the Common Infaunal Species

The assemblages of species described in this chapter had a general similarity with the Amphiura filiformis-Amphiura chiajei mud community off the Northumberland coast described by Buchanan (1963a), a regrouping of Petersen's (1913) Echinocardium-filiformis and Brissopsis-chiajei communities. A more particular similarity exists with the Rhodine facies of the Brissopsis-chiajei association in Loch Nevis described by McIntyre (1961).

The species found common to all four sites were generally cosmopolitan and are found in the same associations as far apart as the Oslofjord, Norway

(Mirza & Gray, 1981) and the Ria de Muros, Spain (Lopez-Jamar, 1981). They were mostly surface feeding species, but also included a number of infaunally burrowing species (Pholoe minuta, Scalibregma inflatum and Notomastus latericeus). Some of these species are favoured by, or are more tolerant to, extremes of environmental conditions. Rosenberg (1977) found that the phoronid Phoronis muelleri and the bivalve Aloidis (= Corbula) gibba were dominant in areas of low dissolved oxygen. Other species, including the bivalve Mysella bidentata, C. gibba and the polychaetes Chaetozone setosa and P. minuta have been found to be typical dominants of sediments with elevated organic content (Pearson & Rosenberg, 1978).

The numerically dominant species may also be favoured by elevated organic content. Of these species Apistobranchus tullbergi showed the highest abundance, but was confined to the Loch Creran site. This is not a commonly distributed species, with only two previous records on the Scottish west coast: in Loch Nevis (McIntyre, 1961) and Loch Creran (Pearson & Stanley, 1977). In a previous survey of Loch Creran, Gage (1972) did not record the presence of A. tullbergi and in the survey by Pearson & Stanley (1977), only low numbers were found (maximum 40 m^{-2}). It is a spionid-like species (Order Spionida - Fauchald, 1977) delicate in nature and probably tubiculous (Pettibone, 1963). No evidence was found in this study of a tube, specimens were fragmented, often with only the anterior part of the body present, tightly curled and with a slight mucous covering. This latter observation may imply inhabitation of a mucus lined burrow. Fauchald & Jumars (1979) noted that members of the family Apistobranchidae were tentaculate, surface deposit feeding and discretely motile. This species has recently been recorded in increasing numbers in Garths Voe, Shetland (Westwood, 1985; Westwood et al., 1987). It was suggested that this area was acting as a limited contaminant sink for hydrocarbons from the adjacent

Sullom Voe oil terminal and that as an opportunist, A. tullbergi was taking advantage of this situation.

Melinna palmata was also highly abundant at the Loch Creran site. As a surface deposit feeder it should also be favoured by a certain level of organic enrichment. Bacescu (1972) noted that in the Black Sea this tubiculous species inhabited poorly aerated soft sediments often under anaerobic conditions with high sulphide levels. This species has also been reported in high densities in the organic rich sediments of Brest harbour (Guillou & Hily, 1983).

The bivalve Thyasira flexuosa found in high numbers at the Loch Riddon site has previously been reported in naturally enriched sediments and those receiving sewage or industrial wastes (Blackstock et al., 1986; Lopez-Jamar et al., 1987). Although this species was previously considered to be a deposit feeder, its feeding mechanism may be specialized. Dando et al. (1985) have found endosymbiotic bacteria in its gills, which, they suggested, probably contributed to its nutrition.

The other bivalve of high dominance, M. bidentata was most abundant at the Loch Creran site, although it was also a dominant at the other three sites. Okelmann & Muus (1978) described this species as being tolerant to a wide variety of conditions. They described its association and burrow sharing with the ophiuroids Amphiura filiformis (principally) and A. chiajei. Its distribution is therefore largely dependent on its hosts. A. filiformis is predominately a suspension feeder (Buchanan, 1964) and will be found in high abundance in soft sedimentary areas of high water flow or enhanced food content in the water column. This species was present in relatively high numbers at all the sites and would probably have been noted as a typical characterizing species of all four macrofaunal communities (Petersen, 1913 - see Chapter 1).

The most abundant species at the Camas Nathais site was the agglutinating Type 1 foraminiferan. This species remained unidentified due to

a lack of expertise with this taxonomically difficult group. It did, however, resemble Crithionina sp. as described by Hoglund (1947) in having a large diameter, irregular greyish shape composed of fine sand grains and lacking a regular aperture. It was unusual to find a foraminiferan to be so abundant in a macrofaunal study as they are usually confined by their size to the meiofauna. However, McIntyre (1961) noted that foraminiferans were the numerically dominant species in both his Fladden and Loch Nevis survey sites. The species at the Loch Nevis site was Crithionina granum with an abundance of 205 m^{-2}, less than the 358 m^{-2} found at the Camas Nathais site. A small number of the type 1 foraminiferan were also recorded at the Creag Isle site, but not in either of the sea loch sites.

The molluscs Corbula gibba and Turritella communis were the two most abundant species at the Creag Isle site. Both these species are ciliary suspension feeders, utilising food particles at the sediment/water interface (Yonge, 1946a, 1946b). As discretely motile shelled species they should be more resistant to disturbance, but as suspension feeders, they may be affected in areas of high resuspension or turbidity.

2.5.3 Megafaunal Burrowers

2.5.3.1 Abundance

2.5.3.1.1 Nephrops norvegicus

The burrows of N. norvegicus were present at all sites. It was the dominant megafaunal species at the Loch Riddon site and least abundant at the Camas Nathais site. This species occurs on most mud grounds throughout the Scottish west coast, supporting an important commercial fishery (Howard, 1982). Abundances vary in different regions; average abundances are: in the Clyde; 0.26 m^{-2} south of the Little Cumbrae (Bailey et al., 1986) and 0.9-14 m^{-2} from Kilbranan Sound (Chapman, 1979), 0.35 m^{-2} in Loch Riddon (Nash et al., 1984), 0.34 m^{-2} off Cloggerhead, East Ireland (Hillis, 1974),

0.9 m^{-2} in the Sound of Jura (Chapman, 1979), 0.23 m^{-2} in the Lynn of Morvern (Bailey et al., 1986), 0.16 m^{-2} from Loch Aline (Atkinson, 1974) and 0.47 m^{-2} from Torridon (Chapman & Rice, 1971). With the exception of Bailey et al. (1986), the actual figures given are for burrow density and not the species abundance. The abundances were calculated from diver transects and remote underwater photography, using the average numbers of openings per individual, recorded by divers. Chapman (1979) has, however, noted the problem of overestimation with this method (for example, he cites the abundance of N. norvegicus as 8 m^{-2} in one area of the Sound of Jura to be an overestimate due to this cause). Hillis (1974) commented that burrow systems in trawled areas possessed more entrances of greater complexity as dispossessed prawns were observed to enter established systems adding on extra branches and openings. Averaged literature values indicate that approximately 29% of these burrows were occupied, although this ranged from 5% south of the Little Cumbrae to 53% off Cloggerhead.

Nash et al. (1984) surveyed both the Loch Riddon and Camas Nathais sites for burrowing megafauna. The abundance of N. norvegicus observed in this study was twice that in Loch Riddon and only a tenth of that reported by these authors for Camas Nathais. Recent increases in fishing activity is the most probable cause of the decrease in abundance at the Camas Nathais site; however, Nash et al surveyed a larger area in their investigations and it is possible that some of the observed differences were due to patch effects. They used a 16 x 16 m grid whereas a 25 x 2 m long transect was used in this survey. Both sets of surveys were done in approximately the same depth range. It is suggested that in Loch Riddon an increase in organic enrichment, as discussed by Pearson et al. (1986a), is having the initial effect of increased abundance of N. norvegicus. Changes in localized fishing effort cannot, however, be ruled out.

Differences in abundance of N. norvegicus between the Camas Nathais and Creag Isle sites was thought to be due to fishing activity. Without heavy fishing activity at Camas Nathais, numbers would probably return to levels recorded by Nash et al. (1984) and be comparable to those at Creag Isle. Bailey et al. (1986) investigated differences in the Firth of Clyde and Sound of Jura populations. In the Clyde where there was a greater proportion of silt-clay and organic content in the sediment, individuals were larger but less abundant. They came to no firm conclusions but suggested either direct or indirect links with the physical characteristics of the areas concerned. If the organic content is too high this would be detrimental to N. norvegicus through a probable reduction in dissolved oxygen. However, the crustacean feeds on a wide selection of macrofaunal species (see Section 3.4.2 for feeding of N. norvegicus) and as macrofaunal abundance may be enhanced by an intermediate level of organic enrichment, so growth of N. norvegicus may also be enhanced. It is possible that Creag Isle represents a low organic site, Loch Riddon an intermediate high level and Loch Creran a level that is too high. Linked with a more flocculant sediment at this latter site, this may have been responsible for the observed low abundance of N. norvegicus.

2.5.3.1.2 Calocaris macandreae

C. macandreae occurred at all the sites and is also common in west coast waters (Nash et al., 1984). Atkinson (1986) reviewed the megafauna of the Clyde and reported densities of 0.8-14.0 m^{-2} in the area, the abundance of which increased with increasing depth of water. Nash et al. (1984) reported 0.04 m^{-2} in Loch Riddon and 0.03 m^{-2} from Camas Nathais. The abundance found in Camas Nathais from this present study was 1.58 m^{-2}. This increase may have been in response to the decrease in abundance of N. norvegicus. Increased area for colonization would be available with decreased interference, as N. norvegicus may predate on C. macandreae (Thomas &

Davidson, 1962; Oakley, 1979; Bailey et al., 1986). Interactions between these two crustaceans are discussed further in Chapter 4. The abundance also increased at the Loch Riddon site which, in a similar fashion to the increase in abundance of N. norvegicus, may be in response to the increase in organic enrichment. Increase in burrow density in relation to depth has been discussed by Nash et al. (1984) and Atkinson (1986). This may have been responsible for the lower abundance of C. macandreae at the Loch Creran site and high abundance at the Creag Isle site. Densities of up to 20 m^{-2} have been reported by Buchanan (1963b) in the deep (80 m) waters off the Northumberland coast.

2.5.3.1.3 Mound-builders

Problems arose with the identification of the callianassid-type mounds as two entities were found to be responsible. Within Loch Creran Callianassa subterranea and Species X were noted (see following section for discussion of the identity of Species X, with respect to similarity of burrow structure to that of other species), whilst at the Creag Isle site only C. subterranea was found. No mounds were identified at the Camas Nathais site and none were cast at the Loch Riddon site leaving minor doubt, though the presence of C. subterranea was noted at both sites on previous occasions (Nash, 1980). These mound-forming species are rarely if ever sampled due to their deep living horizon in the sediment, unlike N. norvegicus and C. macandreae which live relatively near the sediment surface and therefore may be caught by trawling. The abundance of callianassid mounds were recorded in Nash et al. (1984) at 0.29 m^{-2} in Loch Riddon and approximately 0.9 m^{-2} in Camas Nathais bay. If they were present during the course of this present study at Camas Nathais, but in very low abundance, they may have been missed by the relatively small area sampled. Trawling may flatten the mounds but it was thought that these would be rebuilt. Other callianassids have been shown to

rebuild their burrow entrances over a period of a few hours after flattening (Suchanek, 1983). At the Creag Isle site the abundance may have been underestimated as their characteristic galleries were observed in two tier complexes with C. macandreae, but with no surface mounds. The lack of mounds in this case may have been due to the interaction between the two crustaceans.

Abundances of the callianassid type mounds were highest at the Loch Creran site. Callianassids have been reported to be deposit feeders (MacGinitie, 1934) and so would be favoured by some degree of sediment enrichment. Another thalassinid, Axius serratus has been found in large densities in burrows up to 3 m deep in polluted abiotic sediments in the Straits of Canso (Pemberton et al., 1976), but not in adjacent clean sediments. Around the Loch Creran site callianassid mounds were very patchy, but have been observed in densities of up to 10 m^{-2} (Atkinson, 1986).

2.5.3.1.4 Lesueurigobius friesii

The burrows of the goby L. friesii were present at all the sites in similar densities. This species is common in regions burrowed by N. norvegicus (Rice & Johnson, 1972). Abundances were again higher than reported by Nash et al. (1984) in Loch Riddon and at the Camas Nathais site. The highest density was at the Loch Creran site, which may have been due to the high abundance of surface dwelling polychaetes which make up a large proportion of the diet of this species (Gibson & Ezzi, 1978).

2.5.3.2 Burrow Structure

2.5.3.2.1 Nephrops norvegicus

The burrows of N. norvegicus have previously been well described (Dybern & Hoisaeter, 1965; Rice & Chapman, 1971; Atkinson, 1974; Farmer,

1974a, 1974b; Chapman, 1980; Atkinson & Nash, 1985; Atkinson, 1986). The casts obtained in this study were typical of these descriptions.

2.5.3.2.2 Calocaris macandreae

The burrow structure of C. macandreae has also been previously well described (Nash et al., 1984; Atkinson & Nash, 1985; Atkinson, 1986). Again the casts obtained in this study were typical in form of the complex casts described in the literature. All casts were complex with an average of 7 openings per burrow. Nash et al. (1984) described a number of casts one of which had 17 openings. On average, however, they had only 4.7 openings per cast. The average number found by resin casting was not in agreement with that found from the diver transect which underestimated the number. This may have been due to the squeezy bottle technique used, which may not have been powerful enough to reveal all the openings of a burrow. Only one of the burrows had a circular gallery, a feature described by Nash et al. This, they suggested may have implications for an enriched deposit feeding strategy. Deposit feeding in this species has also been discussed by Buchanan (1963b).

2.5.3.2.3 Callianassa subterranea

The burrows of Callianassa subterranea have not been well documented. Their presence has been indicated by volcano-like mounds associated with the burrow entrance. Atkinson & Nash (1985) made reference to these burrows but could only speculate as their casts were often incomplete and the extent of the system unclear. Atkinson (1986) has recently furnished a short description of these burrows. Most of the C. subterranea burrows cast in this study seemed to be complete with a distinct morphology, similar to that described by Atkinson. A vertical shaft of about 1 cm diameter led down from a mound (except in the case of the complex two species casts from the Creag Isle site), to a complex nodular gallery at approximately 40 cm depth. A second shaft

was present in two of the casts, also leading from the surface. In reviewing the morphology of some callianassid burrows, Dworschak (1983) reported a number of different species to have more than one opening. Where a volcano was present, however, the other opening was mostly situated in the close vicinity. None of the other callianassids had a vertical shaft linked to a dense complex nodular system, although de Vaugelas (1984) described two thalassinids of the genus Callichirus, which possessed highly ramified tunnel networks with many blind shafts. Dworschak (1983) noted that most of the callianassids have a continuous burrowing activity, which may well be linked to a deposit feeding mode of life. The callianassids inhabit a range of sediments from shelly sands to fine muds (Suchanek, 1983; Tudhope & Scoffin, 1984; this study). In coarser sediments the burrow galleries may have to extend over a wide area to utilize more dispersed organic content. Higher organic content in finer sediments, however, may lead to the closer linked galleries found in this study. It has also been speculated that the close gallery system is a morphological adaptation to a 'sediment gardening' mode whereby the sediment is enriched with organic detritus to enhance microbial growth for utilisation by the thalassinid (Frey & Howard, 1975; Ott et al., 1976).

2.5.3.2.4 Species X

The burrow of Species X from Loch Creran presented some problems as to its identity. There were two strong possibilities, the thalassinid Jaxea nocturna and the echiuiroid Maxmulleria lankesteri. An individual J. nocturna was dredged up from Loch Creran in the course of this study, indicating their presence. The casts obtained showed some definite similarities to those of J. nocturna recorded by Pervesler & Dworschak (1985) in the Gulf of Trieste, in particular to the top half of one of their casts. The main opening was on a mound, funnel shaped, constricting with depth then broadening as the shaft levelled to the horizontal. Their burrows also showed a tendency to spiral

with depth. There were no branch tunnels, however, which were a characteristic of the burrows of J. nocturna described by Pervesler & Dworschak (1985) and Atkinson (1987). In the horizontal section of some of the Loch Creran casts semi-circular striations were observed on the tunnel roofs. These markings may have been associated more with a hard bodied organisms, for example, the arching of a crustacean abdominal section against the burrow roof, or the lateral imprint of a large bivalve. However, the change in diameter along the length of the cast and the impressions where the cast petered-out were more indicative of a soft-bodied organism. In this respect, M. lankesteri is a strong candidate. In an early unpublished survey of Loch Creran this echiuiroid was present, caught on the anchor flukes of the survey vessel (pers. comm. C. Comely). The constriction of the shaft just below the sediment surface may be the limiting point above which only the narrower proboscis of this species extends to feed. Similar casts obtained from Loch Sween, where M. lankesteri is also present, have contained impressions of this soft bodied vermiform species and identity has been confirmed by both observations and suction sampling. However, to add further complication, Atkinson (1987) reported that some casts which contained J. nocturna were of a simpler structure than those described by Pervesler & Dworschak (1985) and had evidence of the co-occurrence of M. lankesteri, though this latter species was not entrapped in the resin. Definitive identification of species X awaits further evidence. So far, suction sampling and observational night dives have failed to resolve the problem.

2.5.4 Site Differences Due to Organic Enrichment

The prominent factors that were thought to be responsible for the differences between the communities studied were depth, sediment type and organic enrichment. These are not exclusively independent factors; Pearson (1971), Pearson & Rosenberg (1978) and Pearson & Eleftheriou (1981) have

shown that in sea lochs, with increasing depth towards the middle of the loch basins, there are changes in faunal communities, a tendency towards finer sediments, increased organic content and a tendency towards relatively inactive surface deposit feeders. Maurer & Leathem (1981) and Gaston (1987) have demonstrated depth dependence in polychaete feeding guilds, but this was over depths of several hundred metres on the American continental slope and was again correlated to granulometry. It is unlikely that depth differences alone contributed to major differences in community structure between the sites. However, where this factor is linked to sediment type, it may have some effect, especially near the shore, for example, at the Loch Riddon and Camas Nathais sites.

Differences were noted in sediment type, but the sediments of the study sites still fell within the "soft mud" category and were in reality fairly similar. This was evidenced by the large number of co-occurring species. Differences in sediment type or properties (porosity, shear-strength, etc.) may have, however, accounted for the presence or absence of some of the rarer species.

It was thought that organic enrichment was one of the major factors determining the composition of the four soft sedimentary communities. It was further thought that the four sites represented an enrichment gradient with organic content decreasing from Loch Creran through Loch Riddon to Camas Nathais and Creag Isle.

It has been shown in the previous section that the most abundant species were those found at the sea loch sites, which have been associated with organic enrichment. Polychaete guild analysis indicated that these were predominately surface deposit feeding, discretely motile, tentaculate species, for example Apistobranchus tullbergi and Melinna palmata. At the two more open firth sites motile, jawed and soft proboscis type species were predominant, for example Nephtys hombergii and Lumbrineris hibernica. In terms of polychaete biomass, errant polychates made up the greater

proportion of the outer firth sites whilst sedentary polychaetes made up the greater proportion of the sea loch polychaetes. Gaston (1987) noted that the distribution and abundance of surface deposit feeders was regulated by food resources from water column production. Thus, it was felt that differences in feeding type were mostly due to elevated organic levels in the sea loch sites.

The use of single figure diversity indices to categorize and compare different areas has been questioned by Pearson & Rosenberg (1978). They summarize the problems involved with their use, notably that diversity is greatly influenced by sampling and habitat type. Diversity indices were used in this study as a rough guide even though sampling methods were identical and habitat type was similar. Lambshead et al. (1983) suggested that K-dominance curves should be drawn first before any inference is drawn from diversity indices. Use of these curves reveals that some assemblages cannot be compared in terms of intrinsic diversity. When comparing two assemblages only some parts of one species' abundance distribution may be more diverse than the others, but a diversity index may indicate that it has an overall totally different diversity. For example, in this study the diversity (as given by the Shannon-Wiener index) of the Loch Riddon site was between that of the Camas Nathais and Creag Isle sites. Analysis of the K-dominance curve for the Loch Riddon site shows that the more abundant species were less diverse (higher degrees of dominance), whilst the rarer species were more diverse than at either of the other two sites. The K-dominance curve and Shannon-Wiener index both indicated the Loch Creran site to be the least diverse of those investigated. This was thought to be due to the elevated organic content which allowed domination by particular species.

The population statistics also reflect elevated organic content of the sea loch sites (see Table 2.4). The abundance and biomass were both highest at the Loch Creran site, whilst species number was low. This was less evident at the Loch Riddon site where species number was high and biomass was similar

to that of the outer firth sites. The high biomass of the Creag Isle site was thought to be unrelated to organic levels and was explained by the abundance of the heavy-shelled Turritella communis. This abundance ratio, as the number of individuals per species, can given an indication of the carrying capacity of a habitat. Pearson et al. (1986b) havesuggested that the carrying capacity of the benthos is dependent on organic input, whilst it has been shown that the abundance ratio increased along an increasing organic gradient of a sludge dumping site (Pearson, 1987).

The size ratio (average individual biomass) indicates the structure of a community as to the type of species present. A low ratio will indicate the presence of small individuals which may be opportunists with short life histories and high reproductive output. A high ratio is more indicative of larger individuals, long lived, with a low reproductive output (stable climax community). The figure for the Loch Creran site was higher than expected for that of an enriched area. This may have been due to the presence of parts of the heavy tubes of the polychaete Melinna palmata in the biomass measurements. Inclusion of tubes in biomass measurements is questionable. On the one hand, they are not organic tissue: on the other hand, however, they are part of the productive output of the species concerned. In some cases it may be impractical or impossible to successfully separate an animal from its tube. The other figure that may be anomalous was that of the size ratio at the Creag Isle site, where the abundance of T. communis added considerably to the biomass and hence the size ratio. Inclusion of shell mass in biomass measurements may be questioned in a similar manner to the inclusion of polychaete tubes.

The population statistics from different surveys in sites adjacent to the one studied here are shown in Table 2.11. The Loch Creran site of Pearson & Stanley (1977) was very close to that of this study, i.e. within a few hundred

Table 2.11 Population statistics from this study compared with literature values from adjacent study sites, including species number (S), abundance (A), biomass (B), abundance ratio ($^{A}/_{S}$) and size ratio ($^{B}/_{A}$) per square metre.

	Depth (m)	S	A	B	$^{A}/_{S}$	$^{B}/_{A}$	
Loch Creran	16	29.2	3264	220	111.8	70	This study
Loch Creran	16	24.4	1000	51.6	41.0	51.6	Pearson & Stanley 1977
Loch Riddon	22	39.4	2678	92.3	68.5	70	This study
Loch Riddon	40	23.3	1207	60.1	51.8	49.8	Pearson et al. 1986
Camas Nathais	24	36.8	2114	80.9	56.5	40	This study
Creag Isle	26	23.6	872	116.7	36.9	140	This study
LY 1	48	37	468	49.3	12.6	105.3	Pearson et al. 1982

metres. The population statistics from their study are, however, quite different, for two possible reasons. Firstly, no sediment analysis was given in their study. The sediment at their site may have been different, perhaps coarser in nature. Secondly, in the intervening years, the level of organic enrichment may have increased in the loch, perhaps due to an increased output of effluent from the alginate factory. Unfortunately, no data on this were available.

The Loch Riddon site (SK10 - from Pearson et al., 1986a) was investigated in 1974, but the full data remain unpublished. It was approximately 0.5 km out into the loch from the site in this study. Water depth was greater. Again, there was a difference in the population statistics that at first glance may seem attributable to organic enrichment. This would agree with Pearson et al.'s observations that the Clyde system is becoming more enriched. However, this direct comparison cannot be made as there is firstly the complication that sediments become typically finer with depth which may result in a faunal change (Pearson & Eleftheriou, 1981). Secondly, SK10 may have been situated below the well mixed zone and may have been more impoverished from a lack of coupling with pelagic processes.

Th LY1 site was also deeper than the adjacent outer firth sites of this study. Again, the community was more impoverished in terms of abundance, although diversity in terms of species number was high. In common with the Creag Isle site, there was a high biomass in comparison to abundance, leading to a high size ratio indicative of a stable late successional community.

2.5.5 Megafaunal Effects on the Macrofauna

The effects of megafaunal burrow presence on macrofaunal community structure was assessed by comparison of the Creag Isle and Camas Nathais sites. The Creag Isle site was heavily burrowed without much external interference. At the Camas Nathais site, however, fishing activity

maintained a low megafaunal abundance. Diamond (1983) pointed out some of the difficulties inherent in comparing different sites. The major reservation in doing this is that differences may be due to some unspecified factor other than the salient one, in this case megafaunal burrowing activity. Although adjacent, there were slightly differing local conditions at each site. For example, sediment compaction was similar (as observed directly by diving), but their composition was slightly different. However, organic carbon content, which had proved to be an important determining factor at the Loch Riddon and Loch Creran sites was similar at both these sites (approximately 1%).

If the two sites can be compared and the differences were attributable to the presence or absence of megafaunal burrowing species, then it is suggested that these species had a considerable effect on the macrofaunal community structure. Species number, abundance and carrying capacity (as measured by the abundance ratio) were all higher at the Camas Nathais site. Most of the species present at the Creag Isle site were also present at the Camas Nathais site; however, many were less abundant at the former. These included: Foraminifera type 1, Virgularia mirabilis, Lumbrineris hibernica, Cirratulus filiformis, Melinna palmata, Amaeana trilobata, Phascolion strombi and Mysella bidentata.

The low abundance of these species could in some part be explained in terms of megafaunal activity. Benthic foraminiferans feed largely on algae and in some cases have a symbiotic relationship with them (Haynes, 1981). They would thus be confined to the upper few centimetres of the sediment and would be at risk from burial during megafaunal excavations. The burrowing pennatulid V. mirabilis was noted by Hoare & Wilson (1977) to be excluded from disturbed areas. The polychaete M. palmata is a tubiculous surface deposit feeder (Fauchald & Jumars, 1979) and as well as being at risk from burial, its tube would be at risk from disturbance below the surface. A. trilobata is also a surface deposit feeding polychaete, but is discretely motile, not tubiculous

(Day, 1967) and may therefore be able to migrate from areas of stress. The sipunculid P. strombi frequently inhabits the empty shells of Turritella communis (Hylleberg, 1975), from which all specimens obtained in this study were extracted. They have been observed on the sediment surface, the introvert burrowing just below the sediment surface. As they burrow, the shells are pulled along leaving characteristic trail patterns. Their burrowing ability and tolerance to disturbance is poorly understood., The bivalve M. bidentata is associated with the burrow of Amphiura filiformis (Okelman & Muus, 1978); the lower abundance of this latter species at the Creag Isle site would explain the lower abundance of the bivalve.

Biomass and size ratio were higher at the Creag Isle site, due to the abundance of the heavy-shelled Turritella communis. In terms of abundance and biomass composition, Mollusca were the dominant group at the Creag Isle site. Characteristics such as the possession of a heavy shell reducing predation and the ability to reorientate to their living position (Maurer et al., 1986) would protect this group, whilst other less tolerant groups were reduced.

Diversity as measured by the Shannon-Wiener index and the K-dominance curves was lower at the Creag Isle site. Aller & Dodge (1974) also found a decreased diversity due to the bioturbation of Callianassa sp. However, an increase in diversity, abundance, change in community structure and movement of individuals into deeper newly aerated sediments was found by Flint & Kalke (1986) in respect to the colonization of a large burrowing enteropneust. Recently, Posey (1986) found no change in species number in comparing two adjacent areas, one of which was burrowed by C. californiensis. However, he did note that certain species were excluded, notably a number of sedentary spionid polychaetes. These species have previously been reported to migrate from areas of high stress (Levin, 1986).

In this present study there was no noticeable difference between the Creag Isle and Camas Nathais sites in terms of polychaete motility. However,

a higher proportion of omnivore/scavengers were found at the Creag Isle site. This may be in response to the disturbed environment where species are able to utilize a variety of food resources, including unearthed or buried moribund macrofauna, discarded megafaunal prey items or megafaunal faecal pellets.

At Camas Nathais the higher proportion of surface deposit feeders and carnivores may be in response to more stable infaunal conditions and hence wider niche separation. The higher proportion of the former may have been linked to the benthic diatom abundance noted in Section 2.2.3. Increased bioturbation at the Creag Isle site would have a greater disruptive effect on this group of algae.

It was noted in Chapter 1 that megafaunal bioturbatory activity may have two effects on macrofaunal community structure. Community enhancement could be brought about by an increase in sediment/water interface area, and general sediment "conditioning", which involves turnover and aeration. In contrast, surface bulldozing of sediments, turnover in the sediment column, compaction and predation by some of the megafaunal species, may disturb and cause the local extinction of sensitive species.

An increase in surface area of 27% was calculated for the Creag Isle site. This increase in the sediment water interface has an immediate implication for microbial growth. Driscoll (1975) noted that increased depth of the aerobic layer and increase in sediment surface area would lead to an increase in aerobic microbial abundance. As a result of increased sediment water content, there would be an increase in the rate of nutrient mixing and accelerated rates of flushing of metabolites and growth inhibitors out of the sediment also stimulating aerobic bacterial growth rates (Yingst & Rhoads, 1980). Increased microbial growth would lead to an enrichment of the sediment thus providing an increased food resource for deposit feeders. However, a low proportion of deposit feeders was observed at the Creag Isle site. Petersen (1979) has suggested that deposit feeders may be maintained

below the carrying capacity of an environment by other species disturbing the sediment. Once the disturbers were excluded, carrying capacity would be approached. The proportion of deposit feeding polychaetes was higher at the Camas Nathais site, where megafaunal burrowers are partially excluded by fishing activity, which tends to agree with Petersen's theory.

Macrofaunal bioturbation may also be an important factor in regulating the net flux of solutes to and from bottom sediments (Aller, 1982). If this flux was inhibited by megafaunal presence, then solute fluxing may not show an overall increase and may be localized in large burrow linings.

2.5.6 CONCLUSIONS

Megafaunal community composition at the sites investigated was dependent on the local environmental conditions. The important, non-stochastic determining factors seemed to be a complex interaction of organic carbon content, sedimentary characteristics and, to a lesser extent, depth. N. norvegicus and C. macandreae were confined to more compact sediments of an intermediate organic content. The producers of the callianassid-type mounds were confined to sediments of a higher silt/clay content and were more abundant in organic rich sediments. These physical factors, especially that of organic carbon content, were also important in regulating macrofaunal community structure. Megafaunal presence was thought to be responsible for further structuring of these communities on an even more localized scale. As the activity of the different megafaunal species differs, so must their effects. These effects were not isolated but were probably both direct and indirect from sedimentary modifications.

CHAPTER 3. FIELD EVIDENCE OF LOCALIZED DISTURBANCE

3.1 INTRODUCTION

In Chapter 2 it was shown that macrofaunal community structure differed at the experimental sites, even though the general sediment type and fauna was similar. It was suggested that such differences were regulated primarily by two interlinked processes: interaction with the megafauna and the physical process of organic enrichment. In order to investigate megafaunal/macrofaunal interactions in more detail, it was necessary to isolate this interactive process in the field from changing external factors. Controlled sampling on a small scale would then highlight the resultant megafaunal effects on macrofaunal community structure and distribution.

The interaction of megafaunal burrowing species with the sedimentary infauna may result in a considerable effect which could be termed a natural disturbance. This type of disturbance is defined by Zajac & Whitlach (1982) as an "event initiating species populational change either from density independent mortality and/or a change in the resource base of the community". Natural disturbance can differ in time, space and magnitude. An example of large scale disturbance is the occurrence of red tides which occur most often with the spring phytoplankton bloom, and have caused the defaunation of large areas (Simon & Dauer, 1977). In contrast, most biologically caused natural disturbances are typically of small scale, of the order of a few square metres or centimetres. Epibenthos or bottom feeding fish disturb the sea bed during feeding. For example, pit digging has been described for skates and rays (Cool, 1971; Grant, 1983; VanBlaricom, 1982), horseshoe crabs (Woodin, 1978, 1981), edible crabs (Thrush, 1985, 1986), and gray whales (Oliver et al., 1984).

Disturbance of soft bottoms is also caused by the biogenic reworking of infaunal species such as thalassinids for example Upogebia spp. (Ott et al.,

1976; Brenchley, 1981, 1982) and Callianassa spp. (Aller & Dodge, 1974; Ott et al., 1976; Suchanek, 1983; Murphy, 1985; Posey, 1986), enteropneusts (Thistle, 1980; Flint & Kalke, 1986) and acorn worms (Grant, 1983). Of these authors, however, only a few have investigated the effects of burrowing on macrobenthic community structure. For example, Brenchley (1981) by experimental addition of Upogebia pugettensis to enclosures, Flint & Kalke (1986) by monitoring during which an enteropneust population appeared and disappeared and Posey (1986) who assessed the role of Callianassa californiensis in the process of trophic group amensalism. General "bulldozing" has been suggested as being responsible for the evolution of some modern marine benthic communities, in particular the increased diversification of deposit feeders (Thayer, 1979). Thistle (1981) and Probert (1984) have recently reviewed many disturbance processes and their effects on soft bottom communities, the latter noting that: "1. natural disturbance especially biologically mediated disturbances help maintain spatio-temporal heterogeneity of communities and 2. biogenic modification of sediment can affect stability and hence community organization particularly in macrofaunal trophic structure".

Of the megafaunal burrowers described in Chapter 2, both Nephrops norvegicus and Calocaris macandreae occurred at the proposed study site in low, but significant densities. N. norvegicus was chosen as the disturbance agent, however, as its burrows were easily identifiable compared to those of C. macandreae. They are also sizeable enough to take a large number of replicate samples around. Unlike other epibenthic foragers, it produces a burrow and continually reworks it. This is comparable to the thalassinids and enteropneusts previously described. However, due to bulldozing around its burrow entrance and foraging in the near vicinity, N. norvegicus has a wider ranging scale of impact.

To assess the localized effect of N. norvegicus within a community, two areas in close proximity were sampled by replicate diver coring: one around and through a N. norvegicus burrow and the other for comparative purposes, in a visibly unburrowed area. Sedimentary characteristics and macrofaunal community structure were analysed to relate differences to the presence of the burrow.

3.2 MATERIALS AND METHODS

3.2.1 Macrofaunal Sampling

Sampling was carried out at the spar buoy marked site in Camas Nathais bay on two separate occasions (see Section 2.2.3 for site position). Ten replicate diver cores (7.5 cm internal diameter) were taken from two areas approximately 4 metres apart: one set, through and around a N. norvegicus burrow, the other in an area visibly without a major burrow for at least a 1 m radius. It was assumed that large sub-surface burrows did not extend far into this area, that the distance would "buffer" any megafaunal effects and that any differences in community structure between the two areas were due to burrow presence alone. The core spacing was within an 0.25 m radius and they were sunk to a sediment depth of 0.5 m (although friction against the core tube walls allowed core columns not much longer than 0.3 m to be recovered.)

The cores were returned to the laboratory and split into two, the top 10 cm of the core and the rest. Each sub-sample was processed by the methods described in Section 2.3.1. The one exception to this was the use of 0.5 mm sieves at all screening stages.

3.2.2 Sediment Sampling

Two replicate cores were taken in the same sample areas as the macrofaunal cores for sediment analysis. These were returned to the

laboratory and split into three vertical sections where possible: top 10 cm, middle 10 cm and the rest of the core. These sub-samples were analysed according to Buchanan (1984) and Folk (1974), as in Section 2.3.2.

3.2.3 Measurement of Redox Potential

For Eh measurement, 5 replicate diver cores were taken from each of the areas (6 cm diameter, 20 cm length). Each was pushed into the sediment to a depth of 20 cm, although some of this was lost in withdrawal of the core. The cores were returned to the laboratory in chilled insulated containers and were processed within a few hours.

Measurements were taken by the methods described in Pearson & Stanley (1979), using a combined electrode (Russel pH Ltd, Fife, Scotland. Type No. CMPT 11/280/SA1.5). Redox readings were taken 1 cm above the sediment surface, at the sediment/water interface, then in 0.5 cm increments through the core, to 5 cm whereafter 2.5 cm increments were used, since major Eh changes take place in the surface few millimetres (Hargrave, 1972; Pearson & Stanley, 1979).

Data analysis was as described in Section 2.3.4.

3.3 RESULTS

3.3.1 MACROFAUNAL CORES

The full list of the species identified with their respective abundances is shown in Table 3.1. The columns represent the average number of individuals per core, variance and number per square metre. The last column refers to polychaete feeding guilds and is explained later in the text. The lowest abundance per square metre shown for any species present was 25 m^{-2}. This figure was a function of core sample area and averaging across 10 replicates,

Table 3.1 Species list for burrowed and unburrowed sample areas. Values given are for mean core abundance, variation between core replicates (10) and abundance per square metre. Polychaete feeding guilds are explained in the text.

	UNBURROWED AREA			BURROWED AREA			
	Number per core	Variation	Number per m^2	Number per core	Variation	Number per m^2	POLYCHAETE FEEDING GUILDS
Protozoa							
Foraminifera Type 1	3.8	5.9	860	4.2	30	679	
Type 2	1.3	4.9	294	1.1	7	158	
Type 3	7.5	16	1698	37.8	97	2195	
Type 5	0.1	0.1	23				
Type 6	0.3	0.4	68				
Type 7	34.8	299	7877	15.6	230	3531	
Coelenterata							
Pennatula phosphorea (L.)	0.1	0.1	23				
Virgularia mirabilis (Muller)	2.2	2.8	498	2.6	6.0	588	
Varia							
Nematoda sp.	1.8	1.9	407	0.3	0.5	68	
Nemertea Type 1	0.1	0.1	23				
Annelida							
Aphrodita aculeata L.	0.2	0.2	45	0.1	0.1	23	CMJ
Pholoe minuta (Fabricus)	1.8	2.4	407	0.8	0.6	181	CMJ
Eteone sp.	0.2	0.2	45				VMJ
Mystides sp.				0.1	0.1	23	CMJ
Phyllodocidae sp.				0.1	0.1	23	CMJ
Litocorsa stremma Pearson				0.1	0.1	23	CMJ
Synelmis klatti (Friedrich)	0.1	0.1	23				CMJ
Ancistrosyllis groenlandica McIntosh				0.2	0.2	45	CMJ
Ophiodromus flexuosus (delle Chiajei)				0.1	0.1	23	CMJ
Syllis gracilis Grube	0.1	0.1	23				CMJ
Langerhansia cornuta Rathke	0.2	0.2	45				CMJ
Syllis sp.				0.1	0.1	23	CMJ
Exogene spp.	1.3	5.1	294	0.2	0.4	45	VMJ
Nephtys hombergii Savigny	1.2	2.8	272	0.8	0.4	181	VMJ

Table 3.1 (continued)

	UNBURROWED AREA			BURROWED AREA			
	Number per core	Variation	Number per m^2	Number per core	Variation	Number per m^2	POLYCHAETE FEEDING GUILDS
Sphaerodorum gracilis (Rathkle)	0.2	0.2	45				BMX
Sphaerodoridium claparedii (Greef)	0.1	0.1	23	0.1	0.1	23	BMX
Glycera sp.				0.1	0.1	23	CDJ
Dorvillea rubrovittata (Grube)	0.1	0.1	23				VMJ
Lumbrinereis hibernica (McIntosh)	0.9	1	204	0.8	0.6	181	CMJ
Scoloplos armiger (Muller)				0.3	0.2	68	BMX
Spiophanes kroyeri Grube				0.1	0.1	23	SDT
Prionospio malmgreni Claparede	8.2	36	1856	0.5	0.5	113	SDT
Spionidae sp.				0.4	0.9	90	SDT
Magelona filiformis Wilson	0.6	0.5	136	0.4	0.5	90	SDT
Apistobranchus tullbergi (Theel)	2.3	3.6	521	0.2	0.2	45	SDT
Levinsenia gracilis (Tauber)	3.6	6.5	815	2.6	3.1	588	SMX
Paradoneis lyra Southern	2.3	2.7	520	0.5	0.5	113	SMX
Chaetozone setosa Malmgren	0.1	0.1	23	0.1	0.1	23	SDT
Heterocirrus spp.				0.1	0.1	23	SDT
Tharyx marioni (Saint-Joseph)	0.5	0.7	113	0.5	0.7	113	SDT
Cirratulus filiformis Keferstein	0.1	0.1	23				SDT
Cirratulidae sp.	1.5	2.5	339	0.4	0.5	90	SDT
Diplocirrus glaucus (Malmgren)	0.2	0.4	45	0.2	0.4	45	SDT
Cossura longocirrata Webster and Benedict	0.1	0.1	23				BMX
Scalibregma inflatum Rathke	0.2	0.2	45				BMX
Ophelina sp.	0.4	0.5	90				BMX
Notomastus latericeus Sars	0.6	0.7	136	0.1	0.1	23	BMX
Rhodine gracilior Tauber	4.9	5.2	1109	2.1	3.6	475	BLX
Nicomachinae sp.	0.1	0.1	23				BLX
Maldanidae sp.	1.7	16	385	0.5	0.3	113	BLX
Melinna palmata Grube	0.9	2.5	204	0.4	0.3	90	SLT
Terebellidae sp.	0.2	0.2	45				SLT
Euchone sp.	0.1	0.1	23				FLT
Sabellidae sp.				0.2	0.2	45	FLT
Oligochaete sp.	0.3	0.2	68				

Table 3.1 (continued)

		UNBURROWED AREA			BURROWED AREA			
		Number per core	Variation	Number per m^2	Number per core	Variation	Number per m^2	POLYCHAETE FEEDING GUILDS
Sipunculida								
Golfingia elongata (Keferstein)		0.4	0.3	90	0.4	0.3	90	
Phascolion strombi (Montagu)		0.2	0.2	45	0.1	0.1	23	
Crustacea								
Amphipod	Type 1	0.3	0.2	68	0.2	0.2	45	
	Type 2				0.1	0.1	23	
	Type 3				0.1	0.1	23	
Ostracod	Type 1	0.1	0.1	23	0.2	0.2	45	
	Type 2	0.3	0.2	68	1.2	1.5	272	
Tanaid sp.		0.2	0.2	45	0.1	0.1	23	
Cumacea sp.		0.3	0.5	68				
Cirripedia sp.		0.1	0.1	23				
Mollusca								
Chaetoderma nitidulum Loven					0.1	0.1	23	
Hydrobiidae sp.					0.2	0.4	45	
Rissoidae sp.					0.1	0.1	23	
Turritella communis Risso		3.7	11	836	1.4	6.0	317	
Lunatia montagui Forbes					0.1	0.1	23	
Eulimidae sp.					0.1	0.1	23	
Mangelia attenuata (Montagu)					0.2	0.2	45	
Turbonilla lactea (L.)		0.1	0.1	23				
Chyrsallida indistincta (Montagu)					0.2	0.2	45	
Brachystoma eulimoides Henley		0.2	0.2	45	0.2	0.2	45	
Brachystoma lukisi Jeffreys		0.2	0.2	45				
Retusa umbilicata (Montagu)					0.5	0.5	113	
Cylichna cylindracea (Pennant)					0.1	0.1	23	
Hinia incrassatus (Strøm)					0.1	0.1	23	
Philine aperta L.		0.3	0.4	68				
Nuculoma tenuis (Montagu)		0.5	0.5	113	0.3	0.2	68	
Mytilacea sp.		0.1	0.1	23	0.1	0.1	23	

Table 3.1 (continued)

	UNBURROWED AREA			BURROWED AREA			
	Number per core	Variation	Number per m^2	Number per core	Variation	Number per m^2	POLYCHAETE FEEDING GUILDS
Pectinariidae sp.	0.1	0.1	23				
Myrtea spinifera (Montagu)	0.1	0.1	23				
Thyasira flexuosa (Montagu)				0.2	0.2	45	
Mysella bidentata (Montagu)	6.4	45	1446	2	7.8	453	
Eryinacea sp.	0.4	0.7	90				
Dosinia exoleta (L.)				0.1	0.1	23	
Abra nitida (Muller)	0.1	0.1	23	0.1	0.1	23	
Mya truncata (L.)	0.3	0.4	68	0.1	0.1	23	
Corbula gibba (Olivi)	0.1	0.1	23	0.4	0.5	90	
Thracia convexa (Wood)	0.2	0.4	45				
Thracia sp.				0.2	0.2	45	
Spp. indet	0.1	0.1	23				
Varia							
Phoronis muelleri Selys-Longchamps	0.9	0.8	203	0.9	0.8	203	
Echinodermata							
Amphiura chiajei Forbes	0.1	0.1	23	0.1	0.1	23	
Amphiura filiformis (Muller)	0.7	0.5	158	0.4	0.5	90	
Cucumariidae sp.				0.2	0.2	45	

multiplying by a factor of 226 to convert to the number per square metre. Not all individuals could be identified to species level. In the better known groups, this was almost always due to their small size, for example within the molluscs. In other complex groups, for example the oligochaetes and nematodes, specialist taxonomic expertise was not available. The foraminiferans created a particular problem, as several types were identified but not to species level. Type 7 species was a membranaceous allogromiid, Type 6 a calcareous species, whilst the others all possessed an agglutinating test. Of this latter type, Type 1 was unilocular and as discussed in Chapter 2, resembled Crithionina sp. as described by Hoglund (1947). The rest were multilocular. The Type 3 species was probably of the Reophax genus.

A list of the more dominant species with densities in excess of 100 m^{-2} is shown in Table 3.2. Table 3.3 shows the separate rankings for the 25 dominant species from each sample area. Overall the foraminiferans dominated each site in terms of abundance, with the allogromiid Type 7 significantly more abundant in the unburrowed area (7877 m^{-2}). Other species which also exhibited significantly higher abundances ($P < 0.05$) in the unburrowed area included the polychaetes Prionospio malmgreni, Rhodine gracilior, Apistobranchus tullbergi and Paradoneis lyra. The opisthobranch mollusc Retusa umbilicata had a significantly higher abundance in the burrowed area ($P < 0.05$). Although other species also exhibited higher abundances in the unburrowed area, these were not significantly so, probably due to overall low counts in the cores and the small areas sampled.

Thus the rankings in Table 3.3 were dominated by the foraminiferans with 10800 m^{-2} in the unburrowed area. Within the 10 dominant species a greater diversity of groups was found in the burrowed area which included foraminiferans, polychaetes, pennatulids, bivalves, gastropods, crustaceans and phoronids. Only four of these groups were represented in the 10 dominant species from the unburrowed area.

Table 3.2 Numerically dominant species found in the area burrowed by Nephrops norvegicus and an adjacent unburrowed area (with abundance > 100 m^{-2}).

Species	Unburrowed Area	Burrowed Area
Foraminifera Type 7	7877*	3146
Foraminifera Type 3	1698	2195
Prionospio malmgreni	1856*	113
Mysella bidentata	1446	453
Rhodine gracilior	1109*	475
Foraminifera Type 1	860	679
Turritella communis	836	317
Levinsenia gracilis	815	588
Virgularia mirabilis	498	588
Apistobranchus tullbergi	521*	45
Paradoneis lyra	520*	113
Pholoe minuta	407	181
Nematoda sp.	407	68
Maldanidae sp.	385	113
Cirratulidae sp.	339	90
Foraminifera Type 2	294	198
Exogene sp.	294	45
Nephtys hombergii	272	181
Ostracoda Type 2	68	272
Lumbrineris hibernica	204	181
Melinna palmata	204	90
Phoronis muelleri	204	203
Amphiura filiformis	158	90
Notomastus latericeus	136	23
Magelona filiformis	136	90
Tharyx marioni	113	113
Retusa umbilicata	-	113*
Nuculoma tenuis	113	68*

* Significant difference between areas, $P < 0.05$.

Table 3.3 The 25 most dominant Species from the area burrowed by Nephrops norvegicus and an adjacent unburrowed area.

RANK	UNBURROWED		BURROWED	
1	Foraminifera Type 7	7877	Foraminifera Type 7	3531
2	Prionospio malmgreni	1856	Foraminifera Type 3	2195
3	Foraminifera Type 3	1698	Foraminifera Type 1	679
4	Mysella bidentata	1446	Levinsenia gracilis	588
5	Rhodine gracilior	1109	Virgularia mirabilis	588
6	Foraminifera Type 1	860	Rhodine gracilior	475
7	Turritella communis	836	Mysella bidentata	453
8	Levinsenia gracilis	815	Turritella communis	317
9	Apistobranchus tullbergi	521	Ostracoda Type 2	272
10	Paradoneis lyra	520	Phoronis muelleri	203
11	Virgularia mirabilis	498	Foraminifera type 2	198
12	Pholoe minuta	407	Pholoe minuta	181
13	Nematoda sp.	407	Nephthys hombergii	181
14	Maldanidae sp.	385	Lumbrineris hibernica	181
15	Cirratulidae sp.	339	Prionospio malmgreni	113
16	Foraminifera Type 2	294	Paradoneis lyra	113
17	Exogene sp.	294	Maldanidae sp.	113
18	Nepthys hombergii	272	Tharyx marioni	113
19	Lumbrineris hibernica	204	Retusa umbilicata	113
20	Melinna palmata	204	Cirratulidae sp.	90
21	Phoronis muelleri	204	Melinna palmata	90
22	Amphiura filiformis	158	Amphiura filiformis	90
23	Notomastus latericeus	136	Magelona filiformis	90
24	Magelona filiformis	136	Nematoda sp.	68
25	Tharyx marioni	113	Nuculoma tenuis	68

The average species number, abundance and biomass were recorded in Table 3.4 and shown in Figure 3.1. All three parameters were higher in the unburrowed area. Species number was not significantly so, but average abundance and biomass were, at the 1% and 5% levels respectively. A total of 70 species was recorded from each sample area with a maximum number of 31 found in any one core. In the unburrowed area, the biomass of the allogromiid foraminiferan alone was 0.9 gm^{-2}. Although insignificant compared to the total biomass of the area (240 gm^{-2}), it should be noted that much of this latter biomass consisted of molluscan shell weight. The average abundance ratio and size ratios were also recorded in Table 3.4 and shown graphically in Figure 3.2. Again these were both higher in the unburrowed area but this was only significant in terms of the abundance ratio ($P < 0.05$) i.e. each species here was represented by almost 1000 individuals per square metre, almost 70% more than those in the burrowed area.

Differences in community structure between the sample areas were assessed in Figure 3.3, the K-dominance plot (for full explanation see Section 2.3.4). Then x-axis represented the species rank in order of greatest abundance on a log scale, the y-axis, percentage cumulative abundance. The distribution of individuals amongst the species was generally similar. If the two curves were compared more critically, a higher degree of dominance and rarity was exhibited by the species from the unburrowed area, and thus slightly less diversity (dominance is inversely linked to diversity). The species from the burrowed area showed a slightly greater evenness of individuals amongst the species.

As stated in the methods the extruded core length was much shorter than actual penetration of the corer into the sediment (approximately 50 cm depth), mainly due to the design of the corer. The average core length from the unburrowed area was 24 cm and in the burrowed area, 21.8 cm, with variances of 9.5 and 24.4 respectively. The cores were divided into the top 1 cm and the

Table 3.4 Major community statistics for the area burrowed by Nephrops norvegicus and an adjacent unborrowed area (per m^2), including species number (S), abundance (A), biomass (B), abundance ratio ($^A/S$), size ratio ($^B/A$) and total number of species recorded. Means are from 10 replicates.

Levels of significance are: N.S. = not significant, * = $P < 0.05$, + = $P < 0.01$).

	Unburrowed Area	Burrowed Area	Significance
Species No./m^2 (A)	24.6	20	N.S.
Abundance /m^2 (B)	23518	12449	+
Biomass g/m^2 (B)	239.9 g	146	*
Abundance ratio ($^A/S$)	928.8	621.4	*
Size ratio (g) ($^B/A$)	0.017	0.011	N.S.
Total No. Spp. recorded	70	70	N.S.

Figure 3.1 Comparison of species number (S), abundance (A) and biomass (B), between an area burrowed by Nephrops norvegicus and an adjacent unburrowed area.

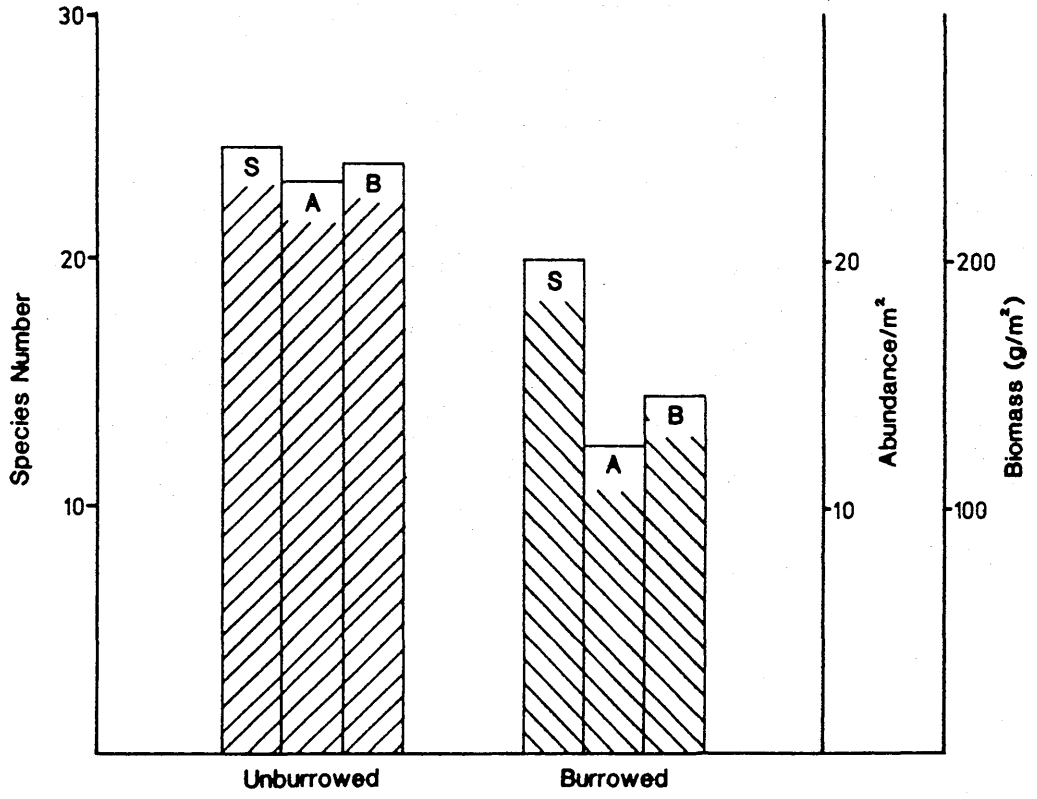


Figure 3.2 Comparison of abundance ratio (A/S) and size ratio (B/A), between an area burrowed by Nephrops norvegicus and an adjacent unburrowed area.

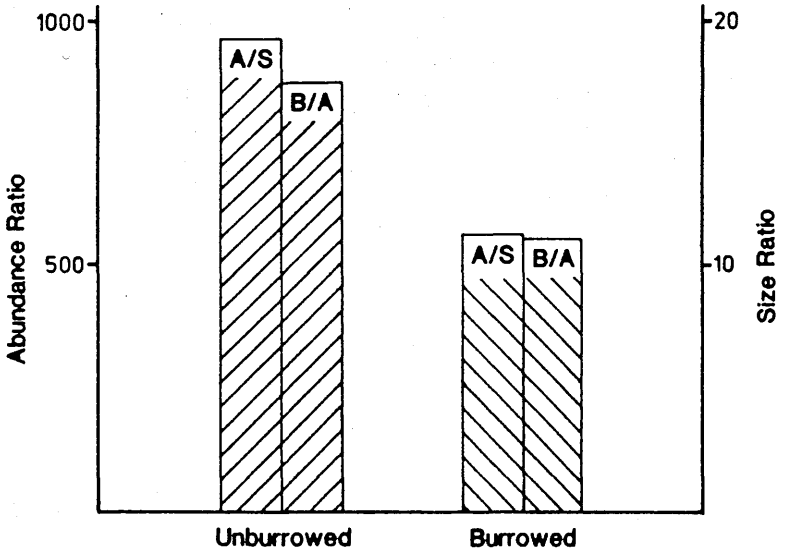
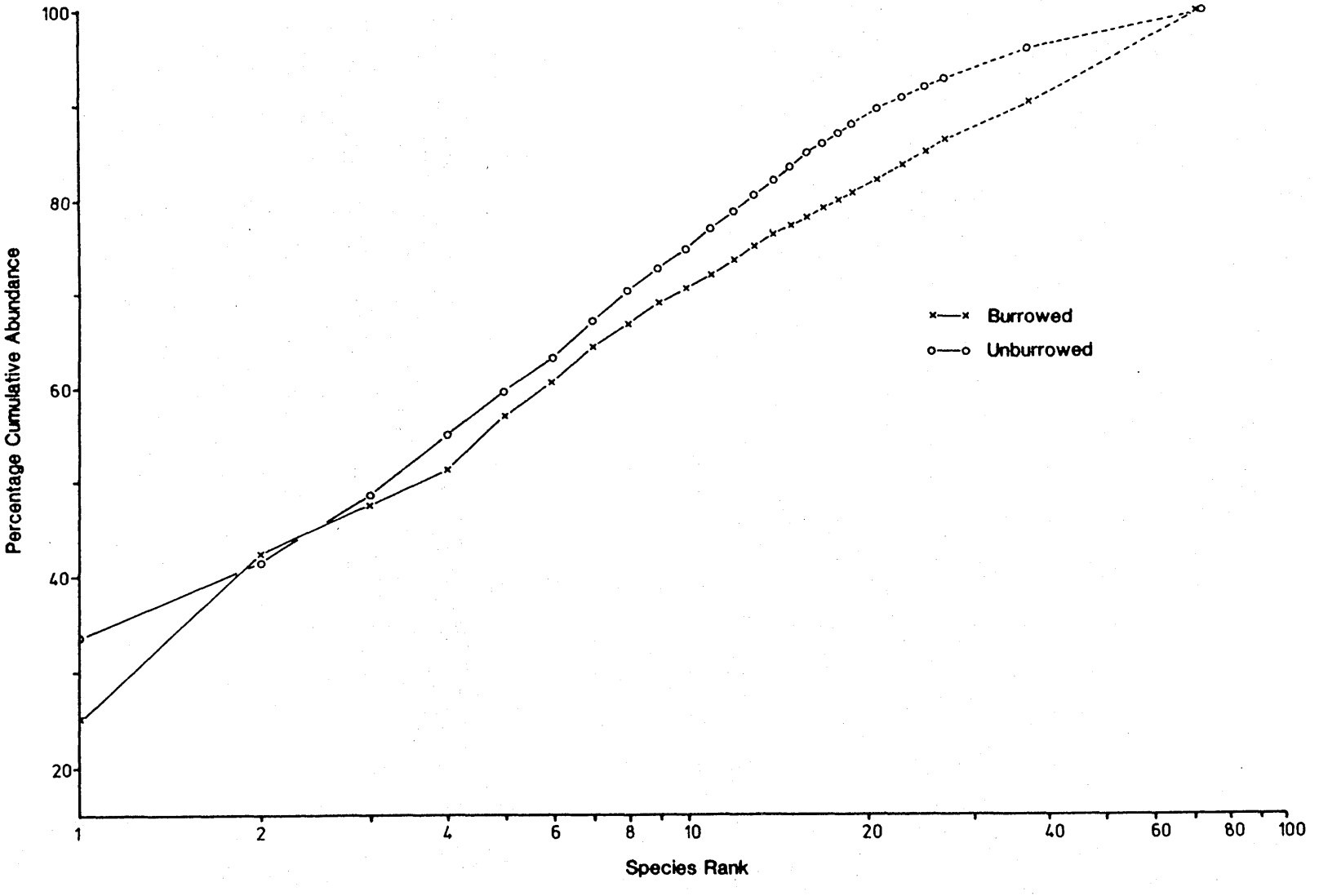


Figure 3.3 K-Dominance plots of the communities from the area burrowed by Nephrops norvegicus and an adjacent unburrowed area.



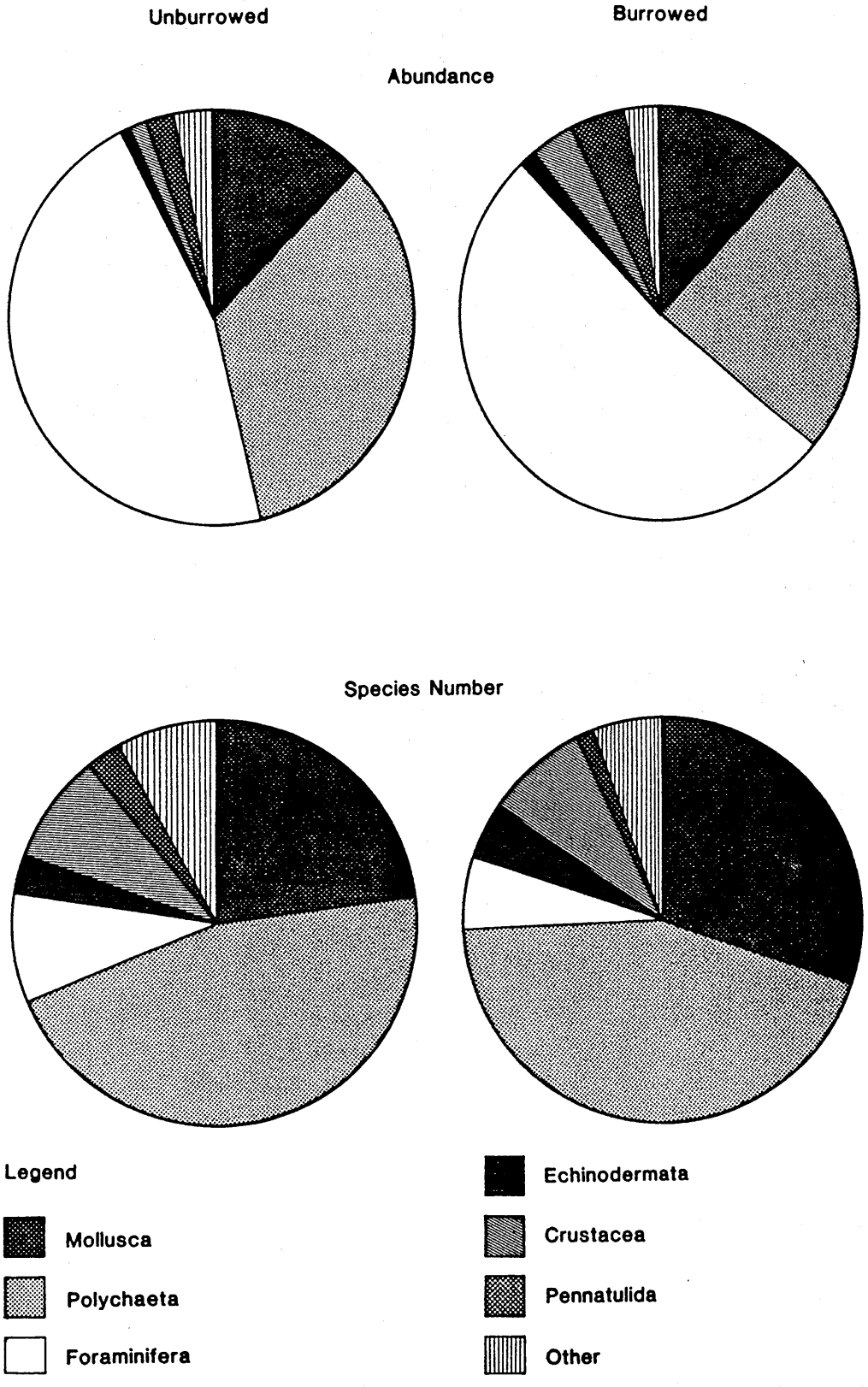
rest, with each section analysed separately. No significant difference was found between the sample areas in terms of distribution of species number, abundance and biomass between the top and bottom of the cores. Average values for the whole area for these parameters below 10 cm in the sediment were as follows: species number 6.6%, abundance 2.4%, biomass 23.1%. The fauna found below 10 cm was mainly comprised of the phoronid Phoronis muelleri and by fragments of large deep burrowing polychaetes (for example, the capitellid Notomastus latericeus and maldanids).

The species and abundance composition of the two sample areas in terms of the major faunal groups are shown in Figure 3.4. Although differences were exhibited, none of these were significant. Foraminifera had the greatest abundance but were represented by only a small number of species. Crustaceans showed the opposite effect of a small abundance made up by a larger number of species. Apart from the foraminiferans molluscs and polychaetes made up the greater part of the abundance and species number in both sample areas. Biomass was not represented here as the fauna was not split into these groups prior to wet weighing.

Investigations of the polychaete feeding categories was based largely on the criteria proposed by Fauchald & Jumars (1979), as explained in Chapter 2. These were:

Feeding Group	1. Subsurface deposit feeder (B)
	2. Surface deposit feeder (S)
	3. Suspension feeder (F)
	4. Carnivore (C)
	5. Omnivore/Scavenger (V)
Motility Group	1. Motile (M)
	2. Discretely motile (D)
	3. Sessile (L)

Figure 3.4 Comparison of the faunal composition of the area burrowed by Nephrops norvegicus and an adjacent unburrowed area.



Morphological Group
1. Jawed (J)
2. Tentaculate (T)
3. Soft proboscis (X)

Each of the polychaetes recorded in Table 3.1 was classified by this method. For example, Pholoe minuta (CMJ) is a carnivorous, motile, jawed species. The percentage occurrence of the different groups is illustrated in Figure 3.5. Differences were observed, for example, the higher proportion of surface deposit feeders in the burrowed area. However, the only significant difference between areas was in the proportion of different mobility types (Chi-squared test $P < 0.05$). The proportion of sessile polychaetes was similar, but there was a higher proportion of more motile species and a lesser proportion of discretely motile species in the burrowed area. This would also account for the high proportion of jawed individuals within the morphological group and carnivores within the feeding group of that area.

3.3.2 SEDIMENT ANALYSIS CORES

The data from granulometric analysis from each core were presented graphically as a cumulative dry weight plot on a probability scale in Figure 3.6 All four curves showed a similar trend. An average of the replicates could have been plotted, but attaching levels of significance to this with only two replicates was impractical. The curves showed no real difference in the coarser area of the sediment distribution but showed some divergence in the area of finer sediments, between 4-8 in phi units, 62.5-3.9 µm. The unburrowed area appeared to have a greater amount of these finer grains. Indices from Folk (1974) of Inclusive Graphic Standard Deviation and Inclusive Graphic Skewness indicated the sediments to be generally very poorly sorted and strongly fine skewed. There was no overall significant difference between the sample areas nor with changes in sediment structure with depth.

Figure 3.5 Pie charts of the composition of different polychaete feeding categories from the area burrowed by Nephrops norvegicus and an adjacent unburrowed area.

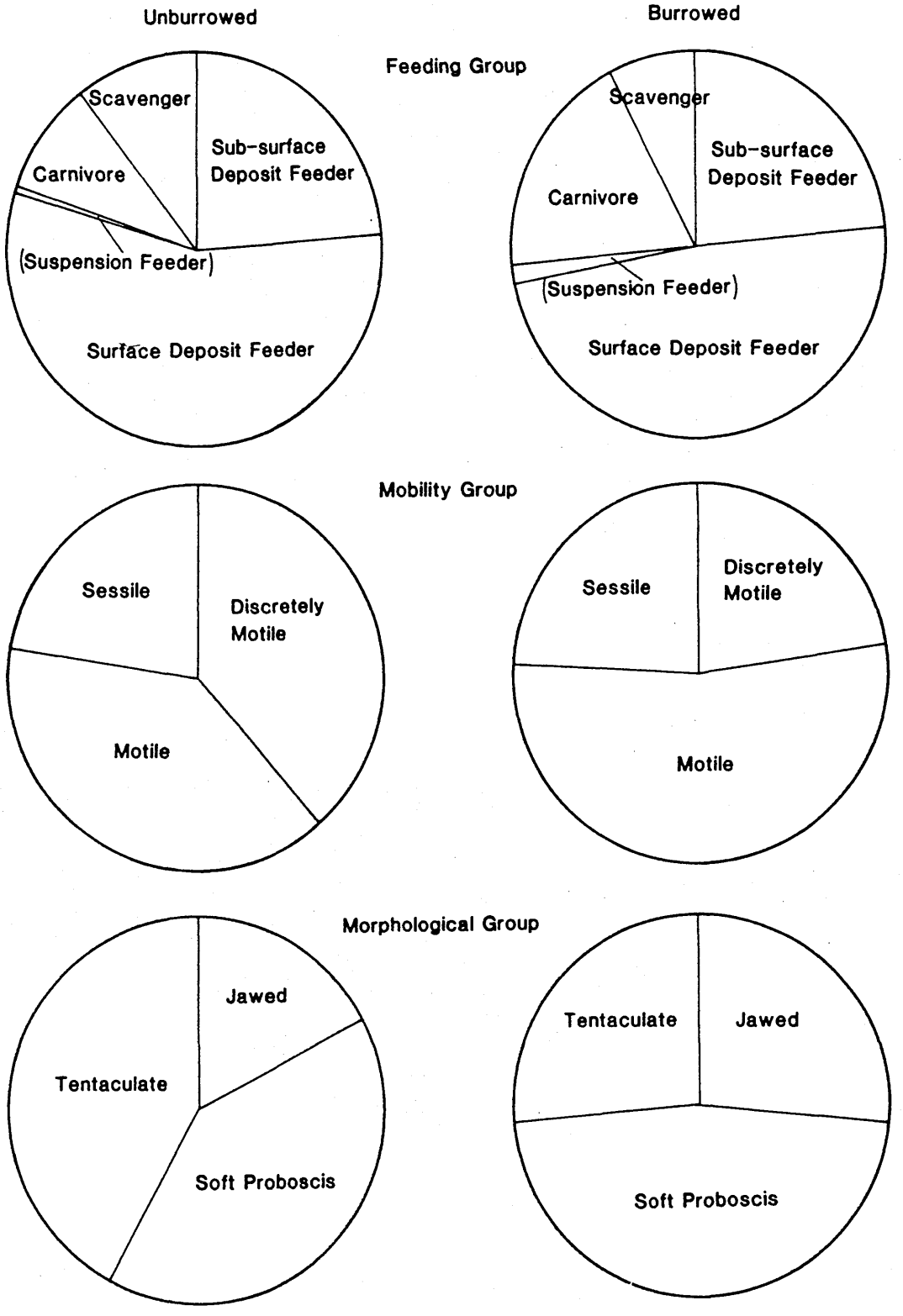
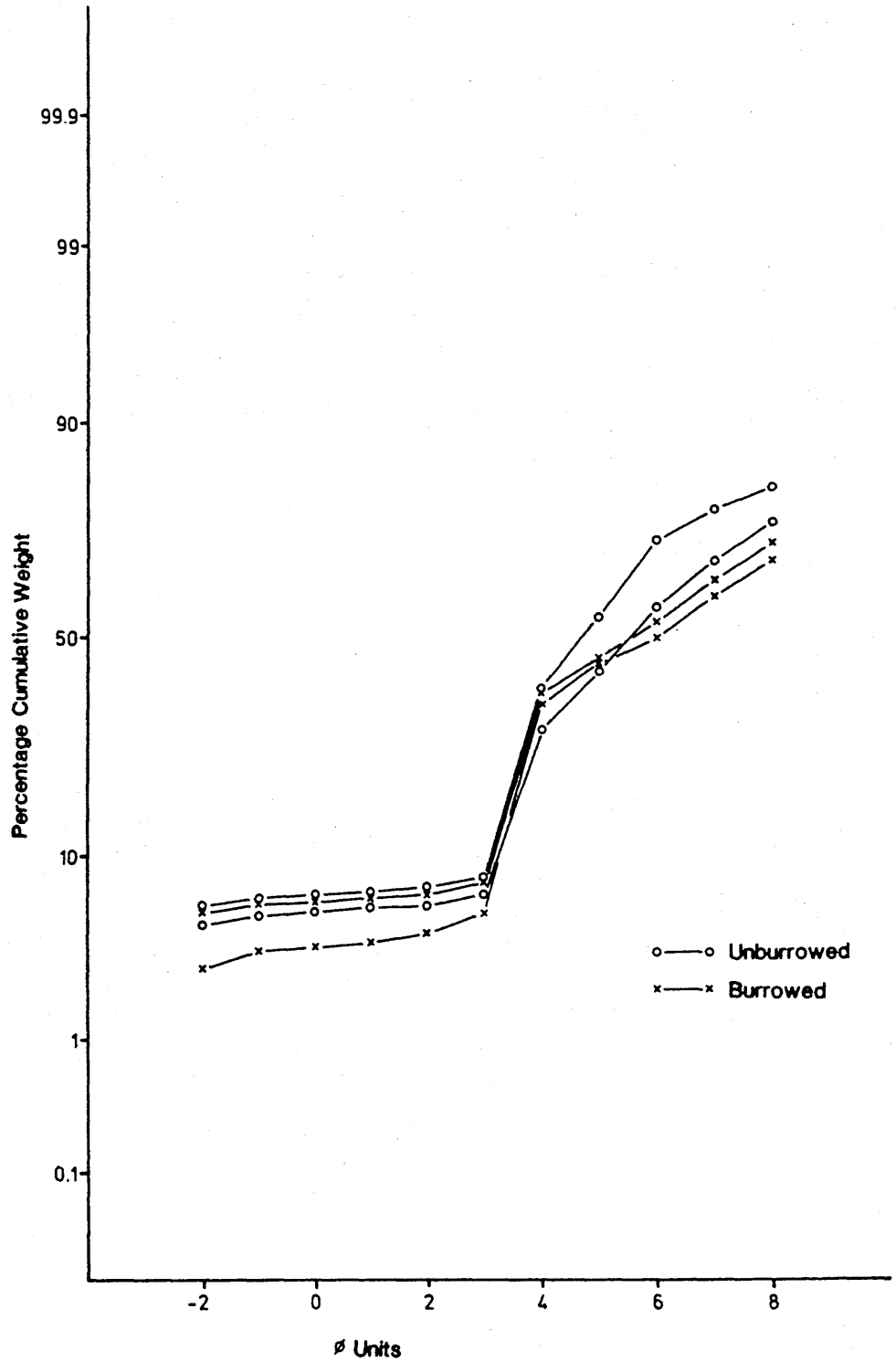


Figure 3.6 Cumulative weight plot on probability scale of sediment grain size distribution from the area burrowed by Nephrops norvegicus and an adjacent unburrowed area.



The median grain size of the separate fractions of the cores was shown in Figure 3.7. At each sediment horizon analysed, the mean and range of the two replicates was plotted. Only one replicate was recovered from the 20-30 cm horizon at the unburrowed sample area.

The probability plots of the combined sub-samples of each replicate showed that there was a greater amount of fine sediment present in the unburrowed area. However, Figure 3.7 indicated that the sediments of the unburrowed area were in fact stratified with depth. A comparatively coarse layer of median grain size 53 μm occurred at the surface, decreasing with depth to 10-20 μm. In contrast the median grain size of the burrowed area indicated finer sediments in the surface layers and generally appeared much more homogeneous with depth, fairly constant in the 20-40 μm size range.

The distribution of organic carbon is shown in Figure 3.8. In the unburrowed area this was fairly homogeneous with depth, constant at 0.9% with little variation. The burrowed area had a greater amount of organic carbon and showed a more heterogeneous depth profile with increased variation. This was approximatly 1.0% at the surface, which increased to 1.2% with a large difference between the two replicates at the 10-20 cm horizon, then decreased with further depth.

3.3.3 REDOX POTENTIAL CORES

The mean values for each set of replicate cores was plotted as two redox profiles in Figure 3.9. Each profile showed a decrease in redox potential with depth. A redox potential discontinuity (RPD) layer occurred in both areas. This varied in depth from just below the sediment surface to approximately 3 cm depth. Both areas had generally similar curves with no significant difference between them. The variation between the replicates was calculated for each depth horizon and was also plotted in Figure 3.9. When compared in a Test for Equal Variances (Conover, 1980, p. 239), significant

Figure 3.7 Change in median grain size with depth of sediment in the area burrowed by Nephrops norvegicus and an adjacent unburrowed area.

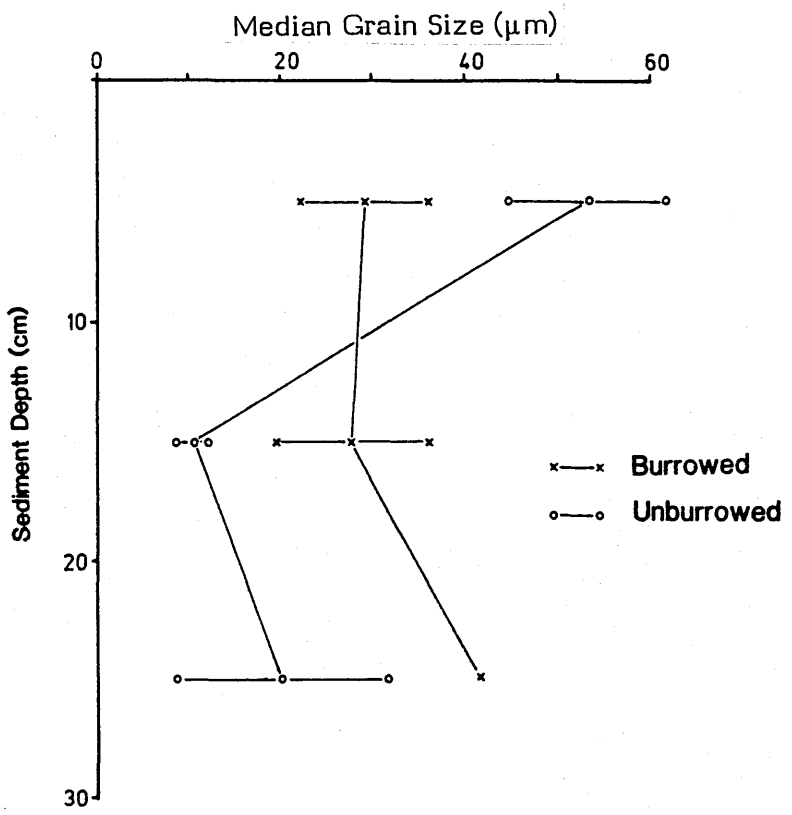


Figure 3.8 Change in organic carbon content with depth from the area burrowed by Nephrops norvegicus and an adjacent unburrowed area. Replicates are joined by their average value.

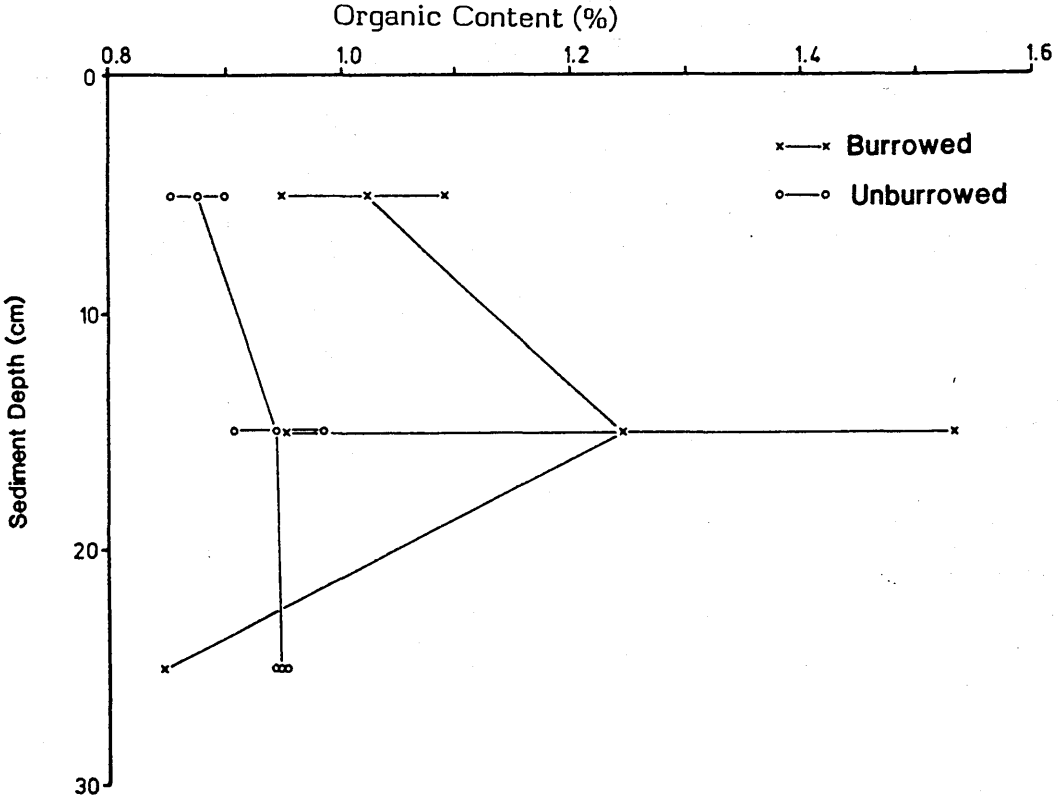
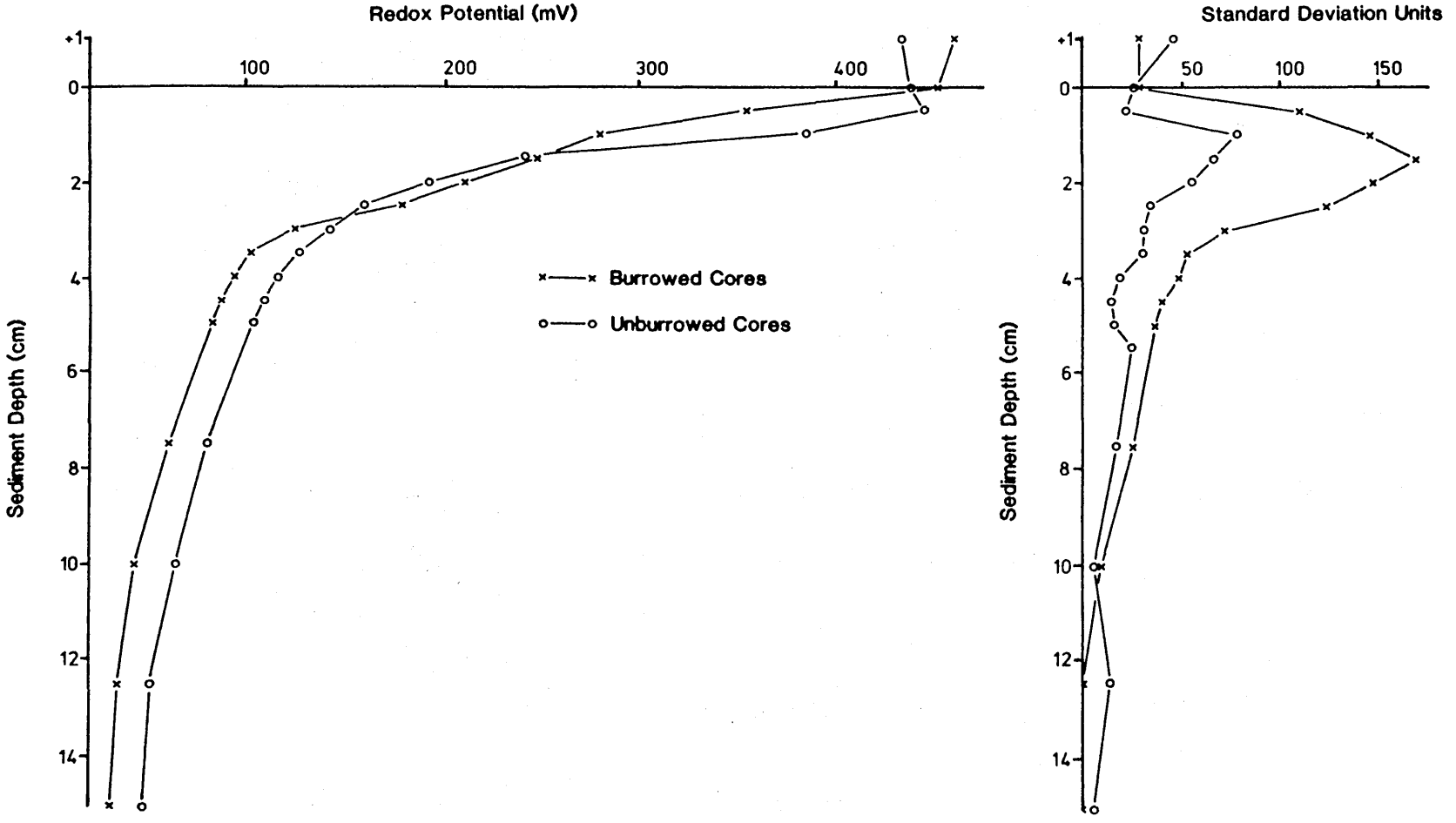


Figure 3.9 Comparison of redox potentials (average of 5 replicates) from the area burrowed by Nephrops norvegicus and an adjacent unburrowed area, with the variation in the replicates plotted seperately.



differences ($P < 0.05$) were found between the sites in the 0.5-2.5 cm sediment depth range, the higher variation in the burrowed area.

The cores for redox potential were pushed approximately 20 cm into the sediment. The maximum core length recovered was 18 cm and the minimum, 11 cm (from the burrowed site). The burrowed site exhibited a significantly higher variation ($P < 0.05$) in core depths presumably due to the disturbed nature of the sediments in the burrow vicinity.

3.4 DISCUSSION

All sampling was done by diver coring, this allowed careful core placement without undue surface sediment disturbance. However, a number of problems were associated with the sampling techniques used. Variation between cores indicated the need for an adequate replicate number when sampling. Of the three types of core taken - macrofaunal, sediment and redox - only the number of sediment cores may have been insufficient to draw fully conclusive results. Stratification of grain size with sediment depth highlighted a problem in sampling for sediment analysis. Care should be taken to sample to an adequate depth of sediment for a true representation of sedimentary characteristics.

If macrofaunal sample size could have been increased, the number of macrofaunal core replicates could have been decreased. Problems with small size were centred around the low number of specimens recovered. The small sample size required the use of an 0.5 mm sieve to collect as many species as possible and consequently resulted in the high abundances of foraminiferans. However, the small core size allowed a large number of replicates to be taken in the immediate vicinity of the burrow.

3.4.1 Burrower Effects on Sedimentary Characteristics

The presence of a N. norvegicus burrow had a significant effect on sedimentary characteristics. Sediment distribution in the unburrowed area showed a degree of stratification indicating lack of vertical mixing processes. The depth profile of the burrowed area exhibited a greater homogeneity with finer sediments in the surface layer, most likely caused by the activity of N. norvegicus in resuspending and mixing sediment, lifting fine particles up to the sediment surface. Callianassa spp. have been observed to modify the grain size distribution within sediments by Suchanek (1983) and Tudhope & Scoffin (1984). It was observed that burrowing action, as well as conveying deep sediments directly to the surface, produced suspended material which then settled in a fine layer blanketing surface dwelling species.

Organic content in the burrowed area had a degree of variability with depth resulting from redistribution of deeper sediments and possible burial of scavenged organic material. Flint & Kalke (1986) observed that the burrowing of the enteropneust Schizocardium sp. caused an increase in organic content with depth. Burial of organic matter has been observed by N. norvegicus in the bottom of its burrow to a depth of 25-30 cm in a glass walled aquaria. This was the reason given by Ott et al. (1976) for the higher than ambient levels of organic matter in the burrows of the deposit feeding crustacean Upogebia pugettensis.

Redox potentials also exhibited greater variation due to the presence of the burrow, deeper aerobic layers and variable organic content in this area. Some of the profiles indicated more anaerobic conditions especially near the surface, which could have been due to relocation of more anaerobic sediments from below, surface compaction, or the inhibition of macrofaunal bioturbatory processes. The latter processes may be of considerable importance in aerating the top few centimetres of sediment (Rhoads & Boyer, 1982).

The core length of both redox and macrofaunal cores showed more variation in depth from the burrowed area than from the unburrowed area. General lack of sediment stability and presence of excavated galleries at depth are the likely cause of this phenomenon which was not observed in the unborrowed area.

3.4.2 Burrower Effects on Macrofaunal Community Composition

Macrofaunal community structure around the burrow of N. norvegicus was quite different from that of an adjacent non-burrowed area. Around the burrow there was a different faunal composition and the community was generally poorer in terms of abundance and biomass.

The species composition of the two areas differed, despite numerical dominance of both these areas by foraminiferans. These were notably the allogromiid naked Foraminifera Type 7 species, with a density of 7877 m^{-2} and a biomass of 0.9 gm^{-2}, the agglutinating unilocular Type 1 species and the agglutinating multilocular Type 3 species. These unfortunately remain unidentified to species level. Foraminiferans may be large in comparison with other Protozoa and some grow up to 190 mm (Boltovskoy & Wright, 1976) although they average about 0.33 mm in diameter (Haynes, 1981). Because of this, they are not normally found in macrofaunal studies but are a major component of meiofaunal samples. The approximate size ranges of the Foraminiferan species found here are: Type 1, 2-3 mm; Type 3, 1-2 mm; Type 7, 1 mm (the sieve used for separation of the fauna had an 0.5 mm mesh). A foraminiferal abundance of $1.1 \times 10^{4} m^{-2}$ was found in the unburrowed area in this study. This would have been a large underestimate of their actual abundance as many individuals would have passed through the sieve. Wallis (1980) working in an adjacent site to the one sampled in this study recorded much higher abundances of up to $2.9 \times 10^{6} m^{-2}$, whilst Hoglund (1947)

measured abundances in the Gullmar Fjord and Skagerak of approximately $1.1 \times 10^7 m^{-2}$.

Allogromiids are common in shallow coastal sediments (Hedley, 1964), and they comprised 63-73% of the Foraminifera abundance in this study. The previous authors, however, only worked on species with permanent hard tests and did not record allogromiids. Gooday (1986) noted that most of the deep sea allogromiids were found in the 0-1 cm surface sediment layer and that it is likely that they sit directly on the sediment surface partially immersed in the uppermost flocculant layer. Agglutinating foraminiferans were found deeper in the sediment. This would explain the significantly less dense allogromiid abundance in the burrowed area, where if they are less likely to burrow they may consequently be unable to relocate to their living position if buried by upheaval or settlement of resuspended material. The agglutinating Types 1 and 3 species showed no significant differences between sample areas, perhaps reflecting their ability to tolerate deeper conditions in the sediment if buried.

Total Foraminifera accounted for approximately 50% of the total abundance. This was represented by only seven species, four of which were insignificant in number and all of which represented 7% of the total species number. The dominant macrofaunal species from sites burrowed by the enteropneust Schizocardium sp. (Flint & Kalke, 1986) were polychaetes, two species of which represented 76% of the abundance. In the burrowed area of this study, polychaetes made up only 24% of the abundance. They had a higher percentage composition in the unburrowed site (34%) but this was only significant at the $P < 0.1$ level. The species composition showed no differences between sites. Both polychaete and mollusc composition were high (45% and 26% respectively). VanBlaricom (1982) found crustaceans to be the most dominant in terms of abundance (50-80%) in sandy sediments disturbed by rays. He did, however, report that molluscs and polychaetes were significantly less abundant in perturbed locations than in control areas.

At the species level, several polychaetes were shown to be significantly ($P < 0.05$) less abundant in the burrowed area. These were: Rhodine gracilior, the spionid Prionospio malmgreni, Apistobranchus tullbergi and Paradoneis lyra. The first three are all tubiculous species. R. gracilior, a maldanid, lives inverted in the sediment and is a deposit swallower (Pearson, 1971). P. malmgreni and A. tullbergi are both bipalpate surface selective deposit feeders whilst P. lyra is a burrowing non-selective deposit feeder (Day, 1967). Amongst the more abundant polychaetes, the tubiculous species seemed more easily disturbed than some of the more mobile species, for example, Nephtys hombergii and Lumbrineris hibernica. From the polychaete guild analysis, sessile individuals seemed unaffected, whilst the proportion of discretely motile individuals was lower in the burrowed area. This latter group included both A. tullbergi and P. malmgreni. It has been noted (Levin, 1982) that some spionids may migrate in response to certain types of stress. Thrush (1985) showed opposite effects on Paradoneis lyra, which showed higher abundances in crab pits than in adjacent unmanipulated areas. This was most likely to be attributable to emigration after the crab digging event, probably responding to freshly turned over organic rich sediment.

Flint & Kalke (1986) showed that the bioturbation of Schizocardium sp. caused a decline in a large population of tubiculous spionid polychaetes. The increase in abundance and species number that followed was due to colonization by small opportunistic polychaetes, for example, the capitellid Mediomastus californiensis and the spionid Polydora caulleri. Posey (1986) showed a negative correlation between three spionid polychaetes (all sedentary tube dwelling deposit feeders) and the presence of C. californiensis. Experimentation by Brenchley (1981) showed that sediment deposition reduced densities of a number of tube building species including a spionid polychaete, with greatest mortality amongst smaller individuals. The presence of the burrowing crustacean U. pugettensis had similar effects. He hypothesized

that relative mobility should be emphasized more when relating bioturbation to benthic community structure (i.e. that disturbance deters sessile species and favours motile species), rather than the previously held model of trophic group amensalism as proposed by Rhoads & Young (1970). This latter theory holds that, by their activity, one particular trophic group may exclude another. For example, deposit feeders may exclude suspension feeders from soft sediments due to environmental modification from their bioturbatory activities. The polychaete guild analysis indicates some agreement with Brenchley's mobility mode hypothesis.

One species, the opisthobranch mollusc Retusa umbilicata showed significantly higher densities in the burrowed area. Little is known of its ecology, but its body form, a smooth cylindrical shell, may be resilient to disturbance (predation and burial) by N. norvegicus, compared to the soft body forms of polychaetes.

At the community level of organization, abundance, biomass and abundance ratio were significantly lower in the burrowed area. Low abundance of infaunal species has been recorded in bioturbated areas by Posey (1986) in relation to Callianassa californiensis and Brenchley (1981) in relation to Upogebia pugettensis and C. californiensis. Flint & Kalke (1986), however, found increased densities and deeper distribution of species in relation to the colonization of the enteropneust Schizocardium sp. In this last study biomass increased and extended deeper into the sediment compared to before Schizocardium colonization. Biomass measurements were not recorded in the previous two studies. In Chapter 2, it was suggested that the abundance ratio gives a measure of the realized carrying capacity of an area, the size ratio, a measure of the size structure of the community. The abundance ratio was higher in the unburrowed area, whereas the size ratio was not significantly different. Thus, no change in the size structure of the community was

indicated and the effect of the burrow/burrower presence was confined principally to the species abundance. It is possible that the unburrowed area acts as a refuge away from the immediate instability of the burrowed area.

Predation may have been responsible for the observed low abundance in the burrowed area. However, N. norvegicus is an active mobile predator and as such could also have foraged out over the unburrowed area, having a similar predatory effect there.

Feeding of N. norvegicus has been investigated by Oakley (1979) in the Irish Sea. He found a large number of taxonomic groups present amongst the stomach contents of the crustacean, dominated by the bivalves Abra spp. and Nucula spp. Several Scottish populations were investigated by Thomas & Davidson (1962) and Bailey et al. (1986). A wide range of groups were represented in the diet, mostly sedentary polychaetes, lamellibranch molluscs, crustaceans, echinoderms (ophiuroids and echinoids) and foraminiferans. The latter were thought to be secondary food items having been derived from the alimentary tracts of larger animals. Most would have been too small (less than 1 mm diameter) to be manipulated directly by N. norvegicus. Thomas & Davidson (1962) suggested that N. norvegicus was for the most part an indiscriminant feeder, taking what it came across when foraging on the sediment surface, stomach contents reflecting seasonal production. In the crustaceans foraging range surface feeding, more sedentary macrofaunal species would therefore be most at risk. Investigation of stomach contents of individual N. norvegicus from the area may have revealed the preferred food items, but it was not possible to do this during the study.

3.4.3 Conclusions

Results demonstrated that macrofaunal community structure and distribution was affected by the presence of the burrow of N. norvegicus.

Major effects were exhibited on the physical and chemical parameters of the burrowed site by the activity of N. norvegicus. Burrowing caused a change in grain size distribution, greater variability in organic content and consequently greater variability in redox potential. Active turn over of sediments and accumulation of mobile finer grains in the surface layers would also give rise to a greater instability in this area. It is suggested that these physical and chemical changes within the sediments were the major cause of the observed differences in macrofaunal abundance and biomass between the burrowed and unburrowed areas. The instability of the burrowed area was reflected particularly in the low abundance of surface feeding, discretely motile, tubiculous polychaetes.

Thus the importance of indirect interactions have been highlighted. The degree of importance of direct interactions, however, could not be assessed by this method of field observation, which requires more careful laboratory observation.

CHAPTER 4. EXPERIMENTAL EVIDENCE OF LOCALIZED DISTURBANCE

4.1 INTRODUCTION

The effects of burrow/burrower presence have been investigated in the field in Chapter 3. Working in the field, one variable such as burrowing can be controlled whilst all minor interactions are maintained. However, there is a possibility that observed differences between the two sample areas were due to either natural variability or an unrecognized factor. Field investigations lack complete control and thus a small degree of uncertainty may be introduced into the results. If the problem of burrow effect was addressed in the laboratory as a single species/burrower interaction, where independent variables such as interspecific interactions can be controlled, then adverse effects could easily be observed. The relevance of such experimentally induced interactions to the more complex natural ecosystem is, however, questionable.

Working within an experimental mesocosm has the benefit of both types of experimentation. The main variable can be controlled and the complexity of the system maintained, whilst reducing natural variability and unpredictable events. Experimental mesocosms have been used in investigations of various degrees of complexity. Major reviews of their use have been accomplished by Boyd (1981) and Grice & Reeve (1982). Most past studies have involved large seawater enclosures for plankton investigations alone. More recently, Berge et al. (1986) have used benthic mesocosms for experimental investigations of sub-tidal soft sediment communities. At the level of complete ecosystems, water column and benthic processes have been linked, for example, by Oviatt et al. (1984) and Kelly et al. (1985).

Experiments described in this chapter were designed to investigate the effect of megafaunal disturbance on macrofaunal community structure in a controlled environment. Secondly, specific interactions were investigated

between burrowers and dominant community members. Nephrops norvegicus and Calocaris macandreae were selected as the disturbance agents. Both crustaceans are typical examples of megafaunal burrowers and are present in the community from which the mesocosm sediment and fauna were collected.

Two experiments were undertaken to mimic the field work presented in Chapter 3. The direct effect of burrows on community structure was investigated by macrofaunal sampling in control and treatment areas, before and after addition of burrowers. The effect of burrowers on redox potential was investigated by following the change in redox during the establishment of a burrow system by N. norvegicus. This latter investigation was not repeated with C. macandreae as the action of using a redox probe repeatedly around its burrow would have a high chance of injuring the animal and may itself cause equivalent change in sediment characteristics.

In conjunction with this, observational work on the redistribution of fauna in relation to disturbance was undertaken, in particular, on the redistribution and activity of Amphiura chiajei. This is a characterizing species of the mesocosm and parent community. Adults are fairly large, with oral disc nearing approximately 10 mm diameter and arm spread 150 mm (Mortensen, 1977). Several aspects of the biology and ecology of this species have been described including: population dynamics, reproduction, feeding, arm regeneration, and burrowing (Buchanan, 1964; Woodley, 1975; Okelmann & Muus, 1978; O'Conner et al., 1983; Bowmer & Keegan, 1983). Only two papers have described interactions with any other species, but these have both concerned commensalism, with the bivalve Mysella bidentata (Okelmann & Muus, 1978) and the polychaete Maldane glebifex (Lopez-Jamar, 1981). A. chiajei is visible from the sediment surface as a number of arms radiating away from the buried oral disc.

A range of other dominant macrofaunal species, notably surface deposit feeders were visible at the sediment surface. It was thought that the response

of these species to disturbance would be representative of that of the rest of the fauna and that by monitoring the visible effect of burrowers on them, the overall effect on the community could be assessed.

4.2 METHODS AND MATERIALS

Much of the experimental work carried out involved manipulations of established sediment mesocosms. These consisted of a number of "living" sediment tanks. A large number of grab samples were taken from the sample site at Camas Nathais bay. The sediment with fauna intact was divided into a number of tanks to an average depth of 25-30 cm. These tanks were provided with a flow through seawater system and housed in a black polythene enclosure, which was illuminated on a 12/12 light/dark cycle by fluorescent light. They were left undisturbed for 20 months for stabilization and compaction of the sediment. Approximately 20% compaction occurred following establishment and prior to the experimental manipulations, mostly in the first 6 months.

Experimentation was conducted mostly in divided tanks, each treatment separated from an adjoining control area by mesh panels. Division within the tanks made statistical analysis of comparative data possible. Numerical comparisons between tanks could not be made due to the slight inter-tank differences in faunal dominance and abundance. Mesh panel dividers allowed emigration of most of the macrofaunal species from the treatment areas as may happen in the field, whilst still containing the megafaunal burrowers.

4.2.1 Effects of Burrowers on Macrofaunal Community Structure

A 1.2 m diameter mesocosm tank was divided into 3 equal sectors with reinforced mesh panels (0.7 cm aperture), which extended from the bottom of the tank to above the overlying water surface. The mesh allowed migration of most macrofaunal animals, whilst keeping the burrowing crustaceans to

their own sectors. The three sectors acted as one control and two treatment areas. Before addition of the burrowers, six cores (core diameter 7.5 cm, penetration depth 30 cm, two cores from each of the three areas), were taken from the tank to assess the pre-experimental tank fauna for comparison with post-experimental samples. To prevent deep flushing and enhanced disturbance through the open core cavities, blank core tubes were retained in each cavity following core extraction. A number of burrowers were added: 3 x N. norvegicus and 2 x C. macandreae to one treatment area and 3 x C. macandreae to the other. The animals were left for 172 days, after which the separate areas were resampled, each with three replicate cores. This number of replicates was adequate for accurate estimates of species number, abundance and biomass and were relatively quick to process. However, this number did prove somewhat low for accurate statistical comparisons of these parameters. Samples were all assessed by the methods described in Chapter 2.

4.2.2 Effects of Burrowers on Redox Potential

A 65 x 50 cm mesocosm tank was divided into two working areas with a reinforced mesh barrier. The area within the barrier acted as a treatment, with a control area outside. Before addition of an individual N. norvegicus, a set of redox profiles were taken from each area by the method described in Pearson & Stanley (1979). A probe stand was supported over the tank on a wooden plank, and the electrode was wound down directly into the sediment. The electrode was 50 cm long and specially constructed by Russel pH Ltd, Fife, Scotland (Number: CMRTTD 11/500). One individual N. norvegicus was added to the experimental area and readings were taken at various time intervals over a period of 4 weeks, when a stable burrow system had been established.

4.2.3 Effects of Burrowers on Amphiura chiajei

Two glass tanks (35 x 20 cm) were filled with defaunated sediment (deep frozen for 48 hours) to a depth of 30 cm and a flow through circulatory system was established. Five individual adult A. chiajei (oral disc diameter, approximately 10 mm) were added to each tank which buried themselves where placed. Two C. macandreae were added to one tank, whilst the other acted as a control. Over the experimental period one of the original C. macandreae died and another individual was added. This individual also died. Finally a juvenile N. norvegicus was added, which killed the original C. macandreae. Burrow system development and the redistribution of A. chiajei were mapped over the experimental period. The relative activity of A. chiajei was recorded over part of this period. A. chiajei is normally a surface deposit feeder (Okelmann & Muus, 1978) and when undisturbed feeds (and respires) with a number of arms fully extended (more than 2 cm of the arms visible on the surface). If disturbed it has been seen to withdraw completely from the surface into the sediment. To observe the effects of disturbance by megafaunal burrowers on this species, its activity was measured by recording both the number of arms fully extended and, also, the total number of arms visible at the sediment surface (fully extended plus those just visible at the surface, but not extended). Observations were made at various intervals over a period of 147 days.

4.2.4 Effects of Burrowers on Surface-Visible Fauna

Two mesocosm tanks (65 x 50cm) were divided into two working areas each with reinforced mesh panels. One area acted as a control and the other a treatment area. Three C. macandreae were added to the treatment area of one tank (T4) and one N. norvegicus to the other (T5). Previous to this, each area was mapped over a period of days by use of a stereo binocular dissecting microscope. A grid system was used to note the position of surface features

and, by making accurate maps, the density and distribution of visible infauna were recorded. The tanks were mapped approximately every 4 days after burrower addition (15 days between the last two dates) for a time period of 40 days. This period was determined by the length of time taken for stable burrow systems to be established.

4.3 RESULTS

4.3.1 Effects of Burrowers on Macrofaunal Community Structure

The positions of the core samples in the mesocosm tank are illustrated in Figure 4.1. Over the experimental period in Sector B, the C. macandreae established a burrow system with several openings which were periodically opened and closed. The N. norvegicus in Sector C did not burrow down but produced a large, deep bulldozed scrape in one corner of their area and another smaller scrape in the opposite corner. The C. macandreae in this sector were killed by the N. norvegicus within a few hours of addition.

The full species list from the macrofaunal cores is shown in Table 4.1. This shows the average core abundance, its variation and abundance per square metre for each species in the sample groups. The lowest abundance for any species identified is 38 in the case of the pre-experimental cores and 75 in the other cores. These relatively high abundances were due to the small size of the cores, and the difference between them, due to the differing replicate number.

Generally speaking, the isolation of the mesocosm tank had resulted in a reduced fauna when compared with samples from the parent community in Chapter 2.

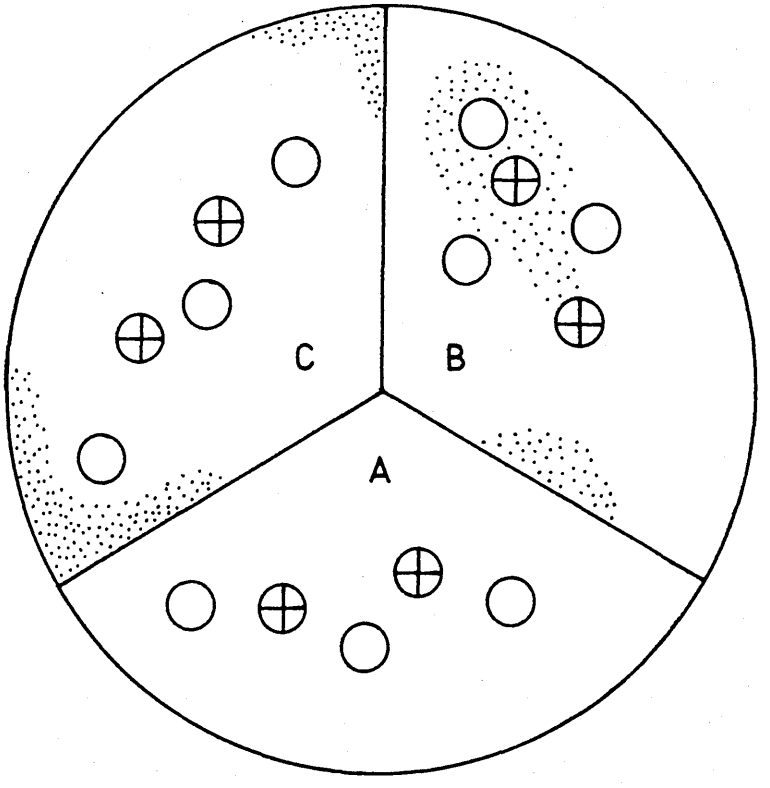
Table 4.2 shows the overall ranked dominant species and the separate 5 dominants for each sector. The Type 3 foraminiferan was the most dominant species of all groups, with a density of approximately 4000 m^{-2} in

Figure 4.1 Core placement in the experimental tank.

A: Control area

B: Treatment area (3 Calocaris macandreae)

C: Treatment area (3 Nephrops norvegicus and 2 Calocaris macandreae)



⊕ Pre-experimental core, blanked off

○ Post-experimental core

Shaded area refers to bulldozed and burrowed areas. Tank has 1.2m diameter.

Table 4.1 Species identified from the different control and treatment areas of the aquarium tank. Values given are for mean core abundance, variation between replicates and abundance per square metre.

		Pre-Experimental Cores			Post-Experimental Cores								
					Control			Calocaris Burrowed Area			Nephrops Burrowed Area		
		Mean No per core	Vari-ation	Mean No per m^2	Mean No per core	Vari-ation	Mean No per m^2	Mean No per core	Vari-ation	Mean No per m^2	Mean No per core	Vari-ation	Mean No per m^2
Protozoa													
Foraminifera	Type 1	0.16	0.16	38				0.3	0.3	75			
	Type 3	38.2	110.6	8639	19.3	101.3	4376	17.7	24.3	3999	20.3	4.3	4602
	Type 5				0.3	0.3	75						
	Type 6	0.16	0.16	38									
	Type 7	0.16	0.16	38	0.3	0.3	7.5	1.7	0.3	377			
Varia													
Nematoda sp.		1.16	2.16	264	2.3	0.3	528	14.3	96	3470	15	49	4150
Nemertea sp.								0.3	0.3	75			
Annelida													
Pholoe minuta (Fabricus)		0.5	0.7	113	1	3	226	0.3	0.3	75			
Langerhansia cornuta Rathke						0.3	0.3		75				
Exogene sp.					0.3	0.3	75	1.3	2.3	302	0.3	0.3	75
Nephtys hombergii Savigny		0.5	0.3	113	0.3	0.3	75	0.3	0.3	75	0.3	0.3	75
Glycera rouxi Andouin & Milne-Edwards								0.3	0.3	75			
Spionidae sp.					0.3	0.3	75						
Magelona filiformis Wilson		1.7	1.5	377	1.3	2.3	302	3	1	679	1.3	0.3	302
Levinsenia gracilis (Tauber)		2	2	453	6.3	0.3	1434	10.3	120	2339	5	7	1132
Paradoneis lyra Southern					2	4	453	2	4	453	0.3	0.3	75
Cossura longocirrata Webster and Benedict					0.3	0.3	75				0.3	0.3	75
Rhodine gracilior Tauber		0.3	0.3	75									
Maldanidae sp.								0.6	1.3	151			

Table 4.1 (continued)

	Pre-Experimental Cores			Post-Experimental Cores								
				Control			Calocaris Burrowed Area			Nephrops Burrowed Area		
	Mean No per core	Variation	Mean No per m^2	Mean No per core	Variation	Mean No per m^2	Mean No per core	Variation	Mean No per m^2	Mean No per core	Variation	Mean No per m^2
Terebellides stroemi Sars							0.3	0.3	75			
Spp. indet	0.2	0.2	38				0.3	0.3	75			
Oligochaete sp.	0.7	2.6	151	2.7	8.3	604	2.3	10.3	528	4.3	12.3	981
Sipunculida												
Golfingia elongata (Keferstein)	0.2	0.2	38							0.3	0.3	75
Phascolion strombi (Montagu)	0.3	0.7	75	0.3	0.3	75	0.3	0.3	75			
Crustacea												
Ostracod Type 1	0.8	0.9	189									
Type 2	4.8	14.2	1094	1.6	0.3	453	0.7	0.3	151	1.7	0.3	453
Mollusca												
Alvania semistriata (Montagu)	0.2	0.2	38									
Turritella communis Risso	4.2	2.6	943	3	1	679	1.3	0.3	302			
Mangelia brachystoma (Philippi)	0.3	0.3	75	0.3	0.3	75						
Brachystomia eulimoides Hanley	0.2	0.2	38	0.3	0.3	75						
Nuculoma tenuis (Montagu)	0.8	0.6	189				0.7	0.3	151	0.7	0.3	151
Nucula sp.	0.7	1.5	151	0.3	0.3	75						
Arctica islandica (L.)	0.2	0.2	38				0.3	0.3	75			
Myrtea spinifera (Montagu)	0.2	0.2	38									
Mysella bidentata (Montagu)	1.6	2.7	377	0.7	0.3	150	0.3	0.3	75			

Table 4.1 (continued)

	Pre-Experimental Cores			Post-Experimental Cores								
				Control			Calocaris Burrowed Area			Nephrops Burrowed Area		
	Mean No per core	Vari-ation	Mean No per m^2	Mean No per core	Vari-ation	Mean No per m^2	Mean No per core	Vari-ation	Mean No per m^2	Mean No per core	Vari-ation	Mean No per m^2
Eryinacea sp.	0.7	0.7	151									
Abra alba (Wood)	0.2	0.2	38									
Corbula gibba (Olivi)	2.7	2.3	604	1	0	266	1.6	2.3	377			
Mya truncata (L.)	0.3	0.7	75	0.3	0.3	75						
Spp. indet	0.2	0.2	38									
Varia												
Phoronis muelleri Selys Longchamps	0.2	0.2	38									
Echinodermata												
Amphiura chiajei Forbes	1.2	0.2	264	1.3	1.3	302	1	0	226			
Amphiura filiformis	0.2	0.2	38	1	3	226	0.7	0.3	151	0.3	0.3	75
Cucumariidae sp.	0.2	0.2	38	0.3	0.3	75						

Table 4.2 Overall numerically dominant species from the mesocosm tank and individual 5 dominant species from each set of cores. Sets of cores were from: pre-experiment (whole tank), control area, area burrowed by *Calocaris macandreae* and area burrowed by *Nephrops norvegicus*.

OVERALL 10 DOMINANT SPECIES

Species	Pre-Experiment	Control	Calocaris	Nephrops
Foraminifera Type 3	8639	4376	3999	4602
Nematoda sp.	264	528	3470	4150
Levinsenia gracilis	453	1434	2339	1132
Ostracod Type 2	1094	453	151	453
Oligochaete sp.	151	604	528	981
Turritella communis	943	679	302	-
Magelona filiformis	377	302	679	302
Corbula gibba	604	226	377	-
Paradoneis lyra	-	453	453	75
Mysella bidentata	377	150	75	-

PRE-EXPERIMENTAL CORES		CONTROL CORES	
Foraminifera Type 3	8639	Foraminifera Type 3	4376
Ostracod Type 2	1094	*Levinsenia gracilis*	1434
Turritella communis	943	*Turritella communis*	679
Corbula gibba	604	Oligochaete sp.	604
Levinsenia gracilis	453	Nematode sp.	528

CALOCARIS CORES		NEPHROPS CORES	
Foraminifera Type 3	3999	Foraminifera Type 3	4602
Nematoda sp.	3470	Nematoda sp.	4150
Levinsenia gracilis	2339	*Levinsenia gracilis*	1132
Magelona filiformis	679	Oligochaete sp.	981
Oligochaete sp.	528	Ostracod Type 2	453

each area after the experimental period. There was no noticeable effect of burrows on this species. The pre-experimental group was totally dominated by this species (with twice the density), whereas other groups showed more even distributions of abundance amongst the species. Amongst the overall 10 dominant species, significant differences in abundances between all the four groups were exhibited, only by the Type 3 foraminiferan and Turritella communis ($P < 0.05$). Nematodes occurred in much higher abundances in the two burrowed areas, but not significantly so. Oligochaetes occurred in fairly high abundance in the sector burrowed by N. norvegicus, compared with the other sectors. Neither live T. communis nor Corbula gibba, however, were found in the cores from this area. The fairly large ophiuroids Amphiura chiajei and A. filiformis were regularly distributed in the mesocosm tank unlike most species (Table 4.1, variance mostly less than mean). A. chiajei was not found in the area burrowed by N. norvegicus, whilst A. filiformis was only present in small numbers.

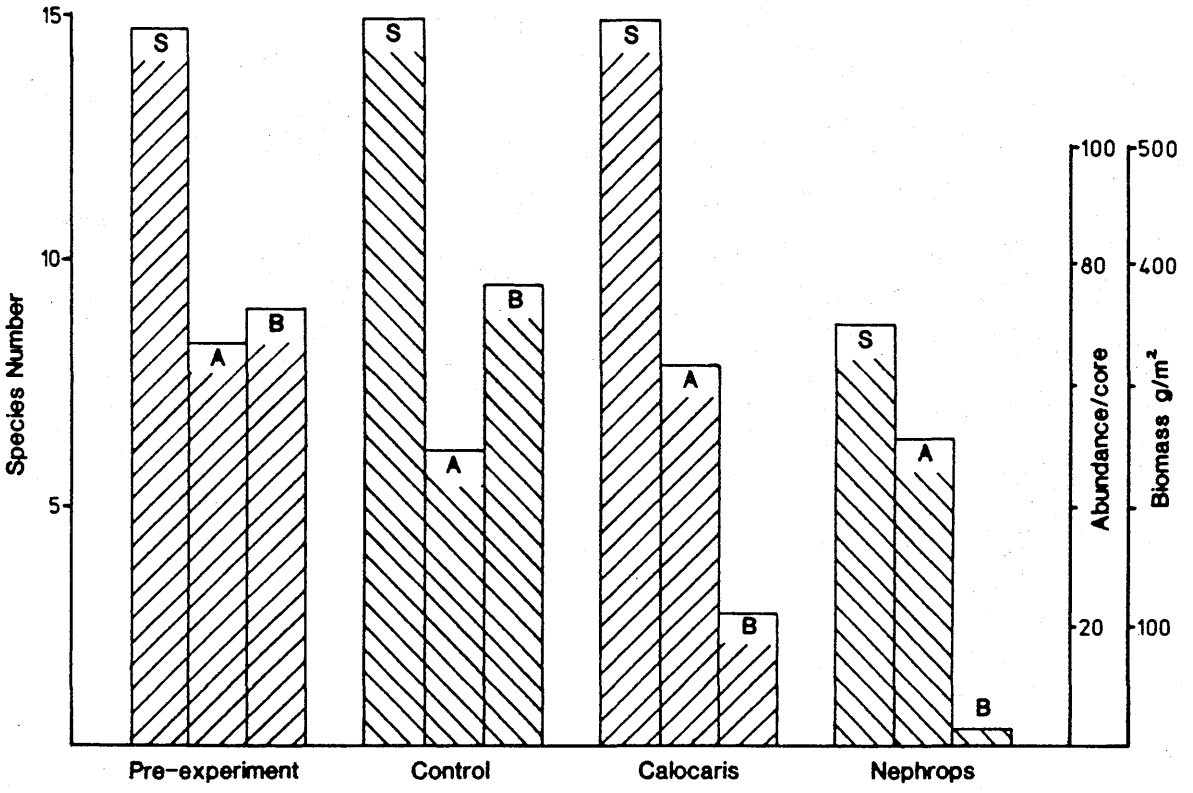
The dominant polychaetes in the mesocosm tank were: Levinsenia gracilis, Paradoneis lyra and Magelona filiformis. L. gracilis occurred amongst the top three species in all except the pre-experimental cores where low abundance kept its relative importance down. Of the post-experimental cores, the abundance of this species was greatest in the area burrowed by C. macandreae (almost twice that of the other two areas). M. filiformis had a similar distribution of abundance in the mesocosm tank. P. lyra was only found in the post-experimental samples and was least abundant in the area burrowed by N. norvegicus.

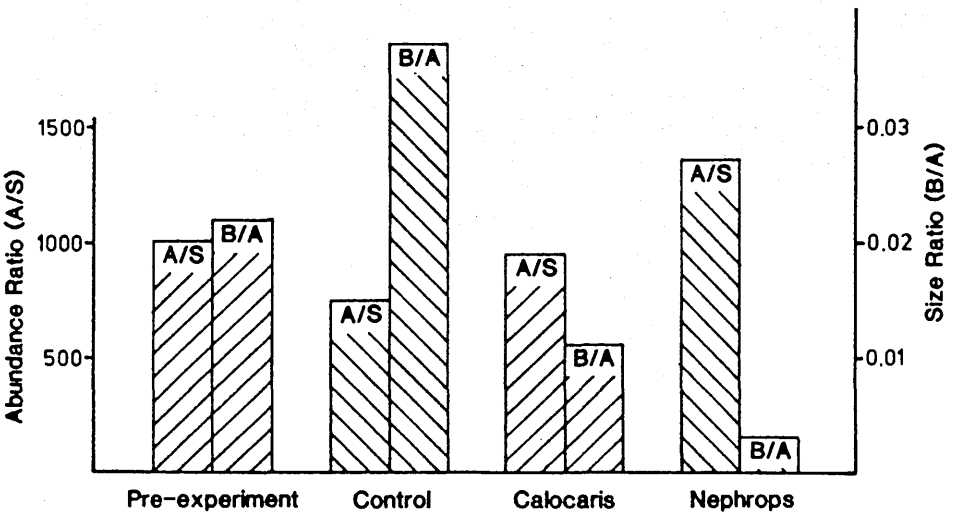
Species number, abundance, biomass and other community parameters are shown for each group in Table 4.3. These are shown graphically in Figure 4.2. A total of 44 species were identified from the cores, with a maximum of 19 from any one core. Average species number was similar for both controls and the area burrowed by C. macandreae, but a decrease in

Table 4.3 Major community parameters from each experimental area of the mesocosm tank.

	PRE-EXPERIMENTAL			CONTROL			CALOCARIS			NEPHROPS		
	$Core^{-1}$	Var.	m^{-2}	$Core^{-1}$	Var.	m^{-2}	$Core^{-1}$	Var.	m^{-2}	$Core^{-1}$	Var.	m
Species Number	14.7	11.8	-	15	3	-	15	3	-	8.7	2.3	
Abundance	66.5	220	15203	49	142	11016	63.3	420	14336	51	169	11
BIOMASS:												
Gastropoda	1.01	0.13	228	1.01	0.13	228	0.09	0.01	19.6	0	0	0
Bivalvia	0.16	0.01	36.2	0.07	0.004	16.6	0.04	0.001	9.1	0.007	0.0001	1
Echinodermata	0.16	0.01	35.5	0.57	0.13	128	0.18	0.007	40.7	0.04	0.006	9
Other	0.09	0.01	21.5	0.03	0.0002	7.5	0.21	0.09	47.5	0.06	0.003	1
Total	1.42	0.16	321	1.68	0.32	381	0.52	0.05	117.4	0.11	0.004	2
Abundance Ratio	-	68261	1058	-	50292	744	-	121736	964	-	254416	1
Size Ratio	-	$5x10^{-5}$	0.022	-	$4x10^{-4}$	0.037	-	$5x10^{-5}$	0.011	-	$4.3x10^{-6}$	0

Figure 4.2 Comparison of species number (S), abundance (A), biomass (B), abundance ratio (A/S), and size ratio (B/A), between pre-experimental area , control area and the areas burrowed by Calocaris macandreae and Nephrops norvegicus





number was found in the area burrowed by N. norvegicus. This decrease was significant ($P < 0.05$).

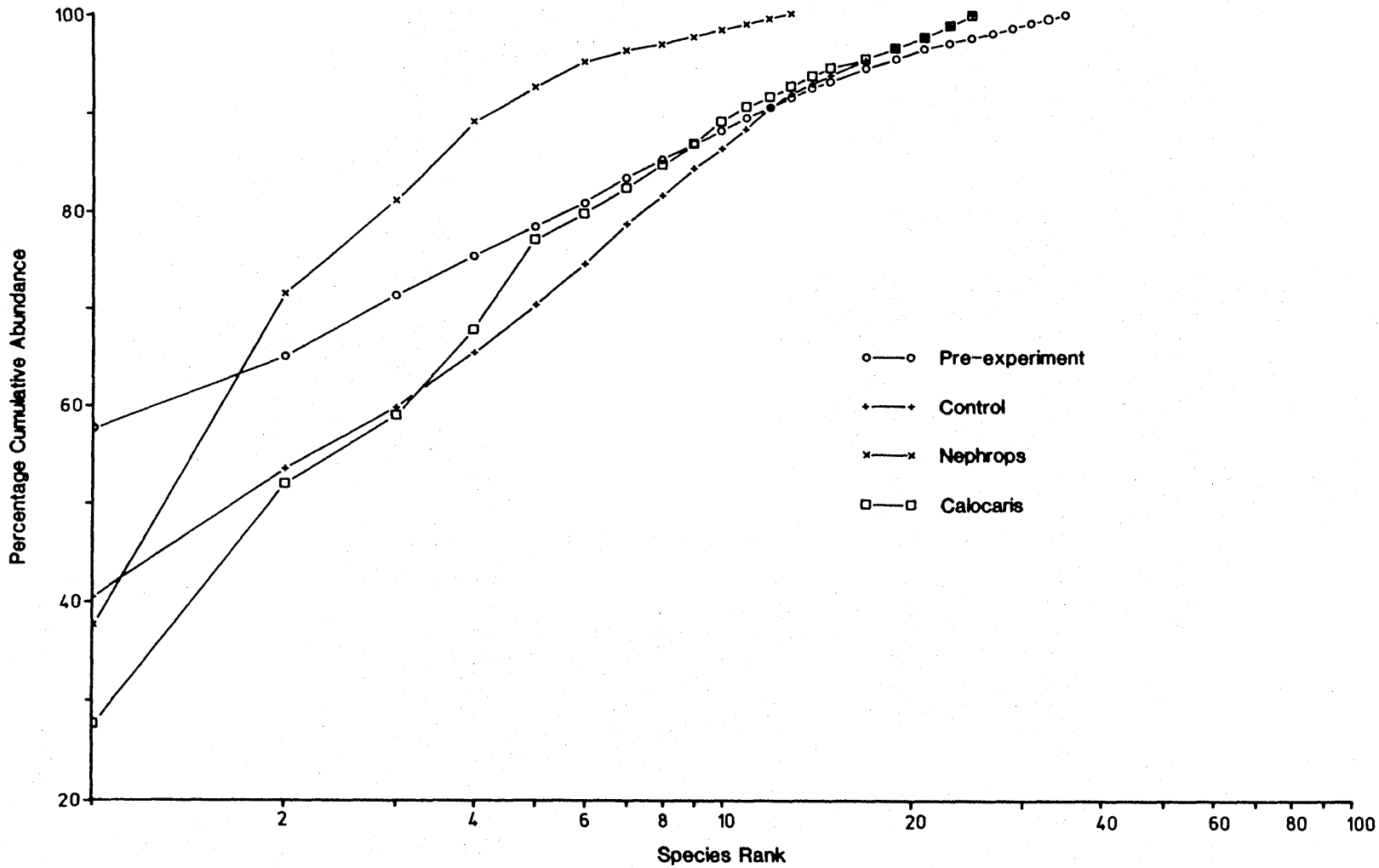
Mean biomass was equivalent in the pre-experimental cores and the control area, but a decrease was observed in the two burrowed areas, with a significant difference between the samples ($P < 0.05$).

Abundance varied between the groups and was seemingly lower in the burrowed areas, but no significant difference was found between them.

There was no significant difference in abundance ratios between groups, with a general value of 1000 individuals per species for the mesocosm tank. A significant difference was observed ($P < 0.005$) between the size ratios of the different groups. An increase in size ratio was found in the post-control group (0.037 g/individual), a decrease in the area burrowed by C. macandreae and a severe decrease was observed in the area burrowed by N. norvegicus, where the average weight of each individual was 0.003 g.

Differences in community structure between the samples was assessed by the use of a K-dominance plot (see Section 2.3.4), shown in Fig. 4.3. The x-axis represents the species rank in order of greatest abundance on a log scale; the y-axis, percentage cumulative abundance. The curve for the pre-control cores starts highest on the y-axis as there was a high degree of domination (57.5%) by the Type 3 foraminiferan species. The curve then rises at a shallow even rate to tail-off gently, as the rarer species had a more even distribution of abundance. The curve for the area burrowed by N. norvegicus rises more steeply as more species share a high degree of dominance. Generally speaking, the higher the curve is to the left, the more dominant the species are and hence the comunity is less diverse (dominance being inversely linked to diversity). The curve for the area burrowed by N. norvegicus is mostly higher than the other curves, so, it can be said to be less diverse. The control and area burrowed by C. macandreae follow each other closely and are of similar diversity. The pre-experimental curve, however, crosses over the

Figure 4.3 K-Dominance plots of the communities from the pre-experimental area, control area and the areas burrowed by Calocaris macandreae and Nephrops norvegicus



other curves as greater diversity was shown at the dominant end of the species distribution but less diversity at the rare end.

The percentage composition of species number, abundance and biomass is illustrated in Figure 4.4. The species composition was similar in the pre-experimental cores and the control area, but there was a shift in dominant faunal group in the two burrowed areas from Mollusca to Polychaeta. This was emphasized more in the area burrowed by N. norvegicus than in the area burrowed by C. macandreae.

In terms of abundance composition, Foraminifera dominated all the groups, especially so in the pre-experimental cores. Otherwise, nematodes and oligochaetes had the greatest percentage composition in the area burrowed by N. norvegicus, polychaetes and Mollusca in the control area and a transitory composition between these, in the area burrowed by C. macandreae.

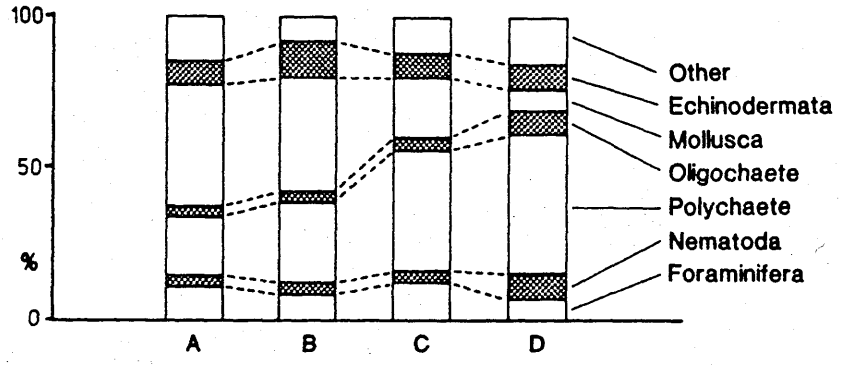
The faunal groups of the biomass composition were slightly different, as species were rough-sorted into these groups prior to wet-weighing and identification. Gastropods, in particular Turritella communis, were dominant in the pre-experimental cores and the control area, but these were of much less importance in the area burrowed by C. macandreae, with none at all in the area burrowed by N. norvegicus.

4.3.2 Effects of Burrowers on Redox Potential

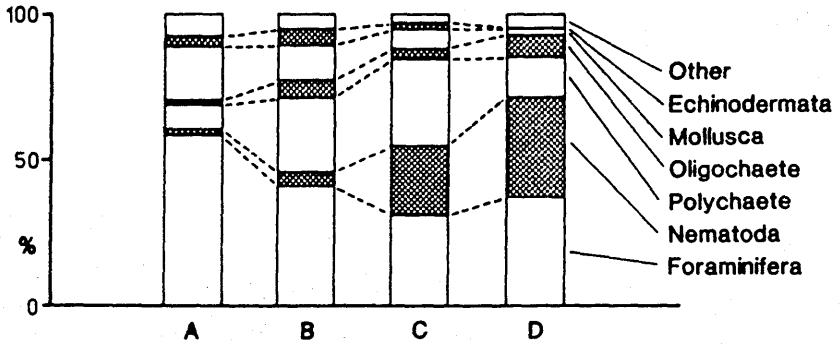
The numbered position of each redox profile measured and the final burrow structure in the mesocosm tank is shown in Figure 4.5. One set of profiles (1, 2 and 3) was taken from both areas before the addition of the individual N. norvegicus. It bulldozed the surface sediment layers along the edge of the tank for a number of days before finally burrowing beneath the sediment on Day 10. The burrow structure was a simple tunnel with "railway-cutting" scrapes at either end. The redox profile from each probing is shown in Figure 4.6. Each pair of graphs represents measurements from the control

Figure 4.4 Percentage composition of species number, abundance and biomass for the pre-experimental (A) control area (B) and the areas burrowed by Calocaris macandreae (C) and Nephrops norvegicus (D).

1. Species Number



2. Abundance



3. Biomass

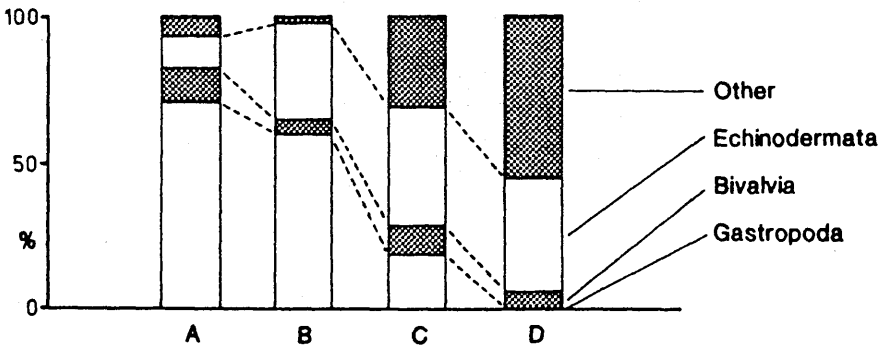
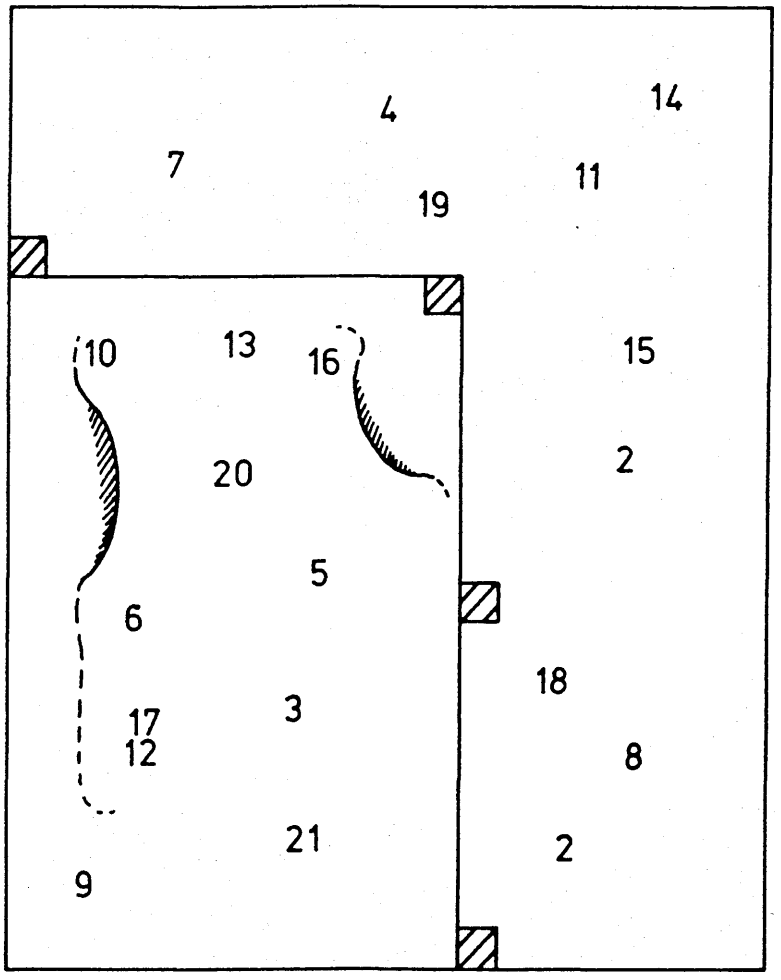
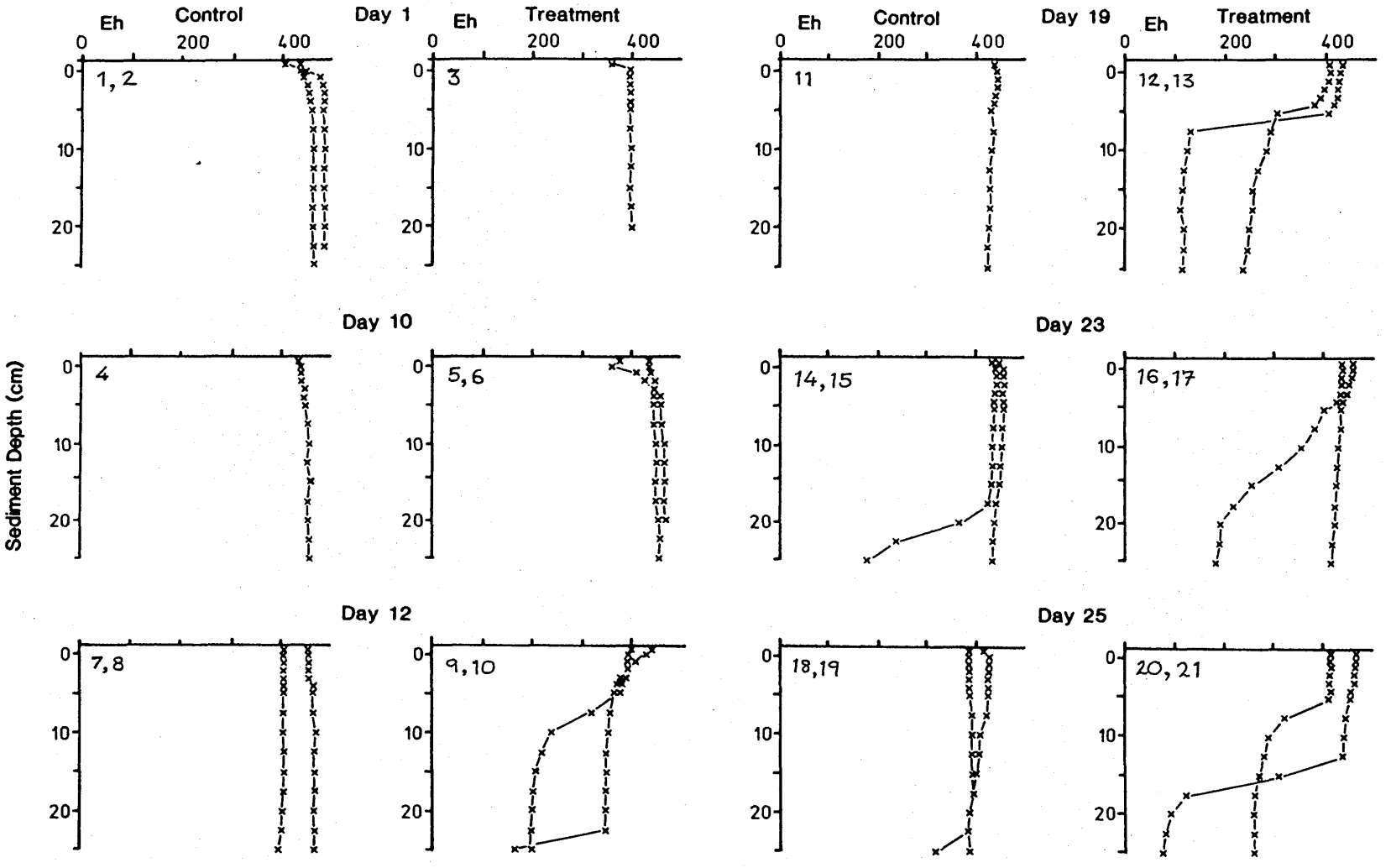


Figure 4.5 Surface of the experimental tank with the position of the numbered redox profiles and the final burrow structure of Nephrops norvegicus (openings indicated by hatched curves). The burrowed area is enclosed by a sunken mesh panel with reinforcing rods shown as hatched squares



DAY	PROFILE NUMBER
1	1, 2, 3
10	4, 5, 6
12	7, 8, 9, 10
19	11, 12, 13
23	14, 15, 16, 17
25	18, 19, 20, 21

Figure 4.6 Change in redox potential (Eh) with time caused by the development of burrow structure by Nephrops norvegicus in the treatment area of the mesocosm tank compared with the control area. Numbers below the intersection of the axes refer to each profile, the position of which is shown in Figure 4.4.



and treatment areas taken over a total time period of 25 days, when a stable burrow structure was established.

The control area profiles show little overall variation over the experimental period. Constant positive redox values of approximately 400 mV were recorded to a sediment depth of 25 cm, with no visible redox discontinuity (RPD) layer. One major exception to this resulted in a final reading of +200 mV, only diverging away from +400 mV below 17.5 cm depth.

The profiles from the treatment area generally showed much greater variation and the formation of an RPD layer. Before Day 10, both areas were similar. On Day 10, in the treatment area, one profile gave an indication of greater negative potentials in surface sediments. After this, all profiles except one showed some divergence from +400 mV to less than +200 mV at depth and less than +100 mV in one case. The one profile that showed no difference to the controls was very near to a previous probing and may have been affected by this sediment disturbance. Surface redox potentials showed little change and the RPD layer in the treatment area occurred below 5 cm sediment depth.

4.3.3 Effects of Burrowers on Amphiura chiajei

External manipulations of this microenvironment were as follows:

DAY	EVENT
1	5 x A. chiajei introduced into each tank, allowed to settle, then 2 x C. macandreae introduced to treatment tank.
6	One C. macandreae dead; was removed.
55	One additional C. macandreae added.
82	Second C. macandreae dead; was removed.
138	Individual N. norvegicus added.
147	End of observations.

Two sets of observations were made at various intervals. The first was involved with the development of a burrow structure and redistribution of A. chiajei, the second with the effect of the burrowers on the activity of A. chiajei.

4.3.3.1 Redistribution of Amphiura chiajei and Burrow Development

Figure 4.7 shows the development of the burrow structures and the redistribution of A. chiajei over the experimental time period. The boxes represent the control and treatment tank surfaces with the crosses marking the position of each A. chiajei. The joined circles represent the C. macandreae burrow shafts and adjoining tunnels.

The number of moves of each A. chiajei was recorded, the total number in the control tank was 10, and in the treatment tank, 13. When the N. norvegicus was added to the treatment tank, two A. chiajei disappeared and were assumed to have been killed by the foraging crustacean. The moves were plotted as a cumulative distance moved in Figure 4.8 for each tank. Although the total number of moves was similar, the distance moved by the A. chiajei in the burrowed tank was 122.4 mm, almost twice the distance moved in the control tank (66.3 mm). A number of specific interactions resulting in movement were observed between C. macandreae and A. chiajei.

One A. chiajei (Day 13) moved into the bottom of a shaft 3 cm deep, formed by the prospecting of the C. macandreae when first added to the tank.

Another individual moved into the spoil heap around the main entrance of the C. macandreae burrow (Day 4) and stayed there for the whole length of the experiment. Sediment from deeper down in the tank was deposited here irregularly throughout the whole experiment.

A third individual moved across the tank when a C. macandreae burrowed down on top of its position (Day 60).

Figure 4.7 Development of the burrows of Calocaris macandreae and Nephrops norvegicus and the redistribution of Amphiura chiajei in the experimental tanks. Views represent the sediment surface.

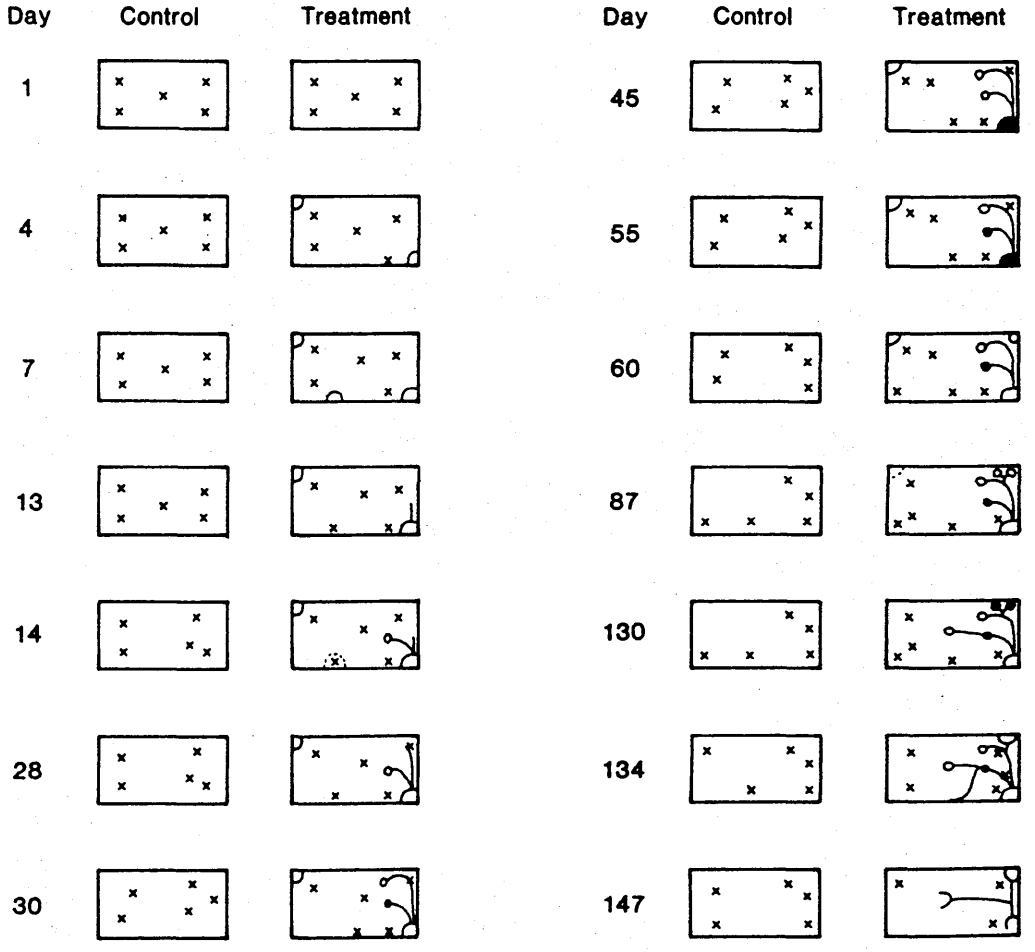
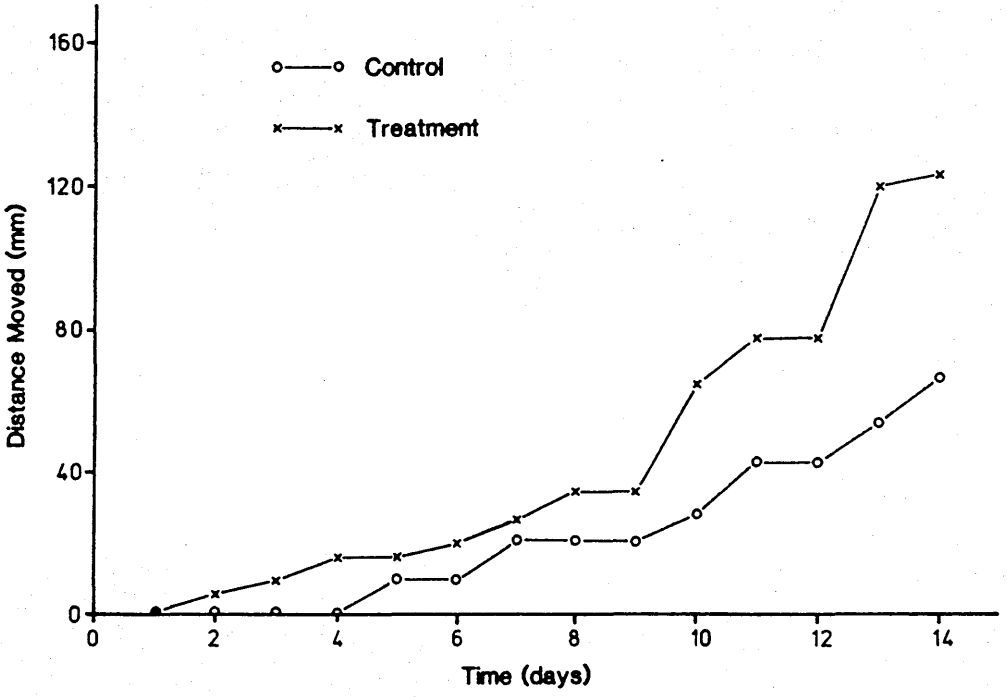


Figure 4.8 Cumulative distance moved by all the Amphiura chiajei over the experimental period



The A. chiajei generally occupied a position in the sediment 3 cm down. This was just in the area of lighter oxidized sediment in the control tank. However, one individual was observed in the oxidized sediment associated with the C. macandreae burrow, at a depth 9 cm.

The development of the C. macandreae burrow system illustrated in Figure 4.7 was as follows:

DAY	EVENT
1	Individuals added to the treatment tank.
4	Animals sitting in small body length shafts.
13	Shaft twice as deep with short side tunnel, i.e. J-shaped.
14	First U complete; excavated sediment left at surface around main entrance and packed into original side tunnel.
28	Extension of original side tunnel.
30	Second U completed.
87	Third U completed, breaking into a surface shaft from below.
130	Fourth U completed, extending off the first U.
137	N. norvegicus added modifying burrow.

The whole C. macandreae burrow was completed by one individual. The two that died did not progress beyond sinking simple body-length shafts. The entrance and other openings of the burrow were opened and closed at irregular intervals that seemed to be unconnected to external factors. However, the presence of a second C. macandreae on the sediment surface caused an increase in the activity of opening up and closing off burrow openings. Closing off an opening consisted of packing it from beneath with one or several loads of sediment which formed a plug.

The observed activity of the C. macandreae was very irregular. It would stay passive within its burrow for long periods of time, occasionally orientated upside-down and only occasionally beating its pleopods to produce a respiratory current. Bursts of excavatory activity lasting up to 48 hours would produce a new U in the burrow system, after which the animal returned to a passive state. This individual was never seen on the sediment surface and no tracks were seen on the sediment surface, suggesting that C. macandreae has a non-emergent lifestyle. It only came to the main entrance to deposit excavated sediment towards the beginning of the experimental period and on rare occasions after that. Appearance at other openings was associated with opening up and closing off. The main gallery horizon was at approximately 8 cm depth with lighter oxidized sediment to 11 cm. When added to the system, the individual N. norvegicus burrowed through the existing burrow belonging to C. macandreae to produce a simple T-shaped burrow at the same sediment depth.

4.3.3.2 Activity of Amphiura chiajei

The activity of A. chiajei was observed and noted as defined in Section 4.2.3. Accurate records were kept from Day 90 onwards, with a 15 day break after Day 93. Normally three sets of observations were made at approximately 0900, 1400 and 2300 hours each day, though this was supplemented with occasional additional observations. No significant difference in activity was noted across the 24 hour period of observations, nor was any change noted in the control. Therefore, a mean measure of activity was taken for each set of daily observations. Figures 4.9 and 4.10 show the change in activity in terms of the total number of arms at the sediment surface and the number of these arms that were extended, actively, foraging. Since the tank contained 5 individual A. chiajei, the total number of arms in each tank was 25 assuming each animal to be still intact. The maximum

Figure 4.9 Change in the total number of arms visible of Amphiura chiajei at the sediment surface in the control and treatment (burrowed area).

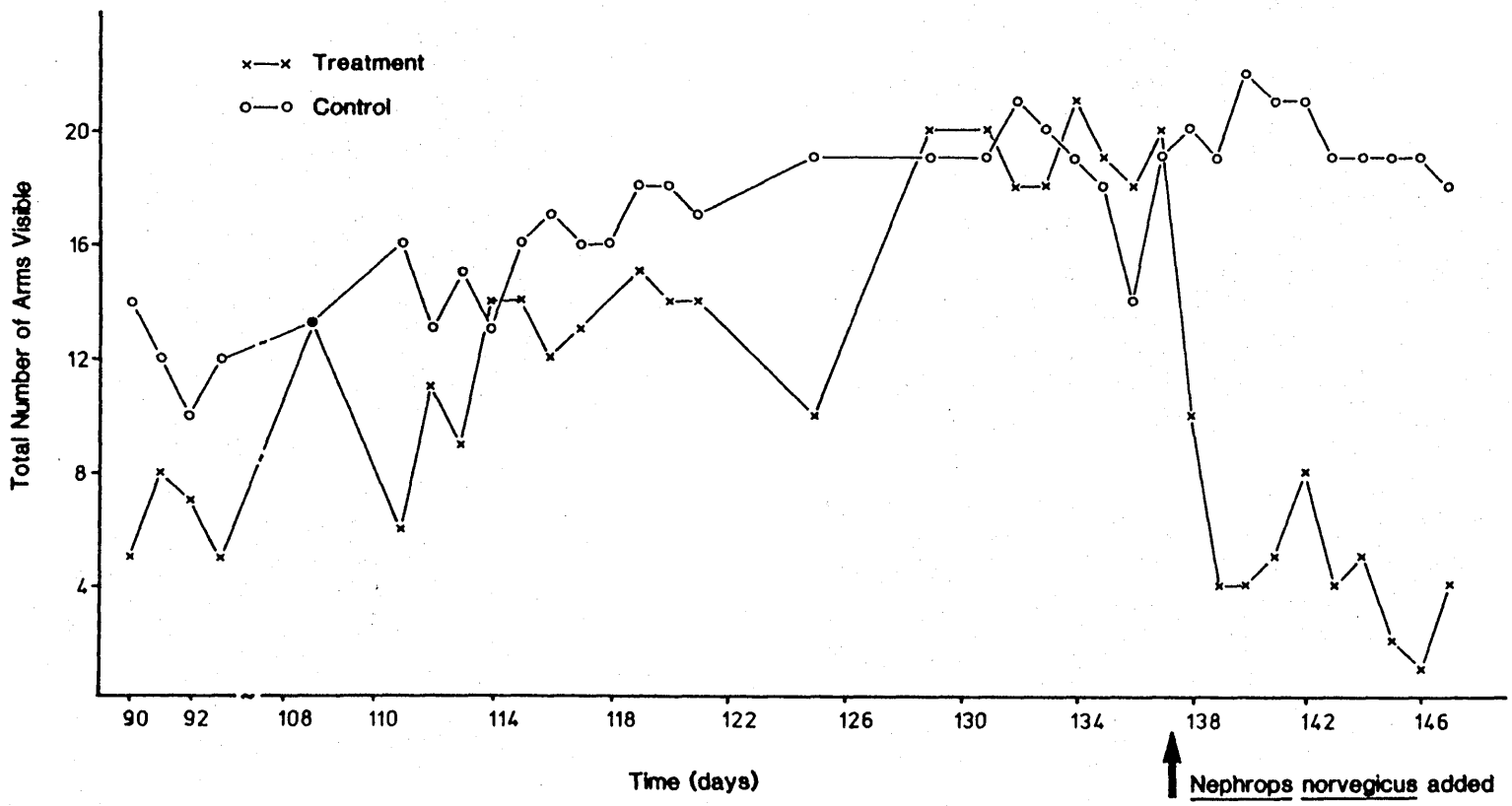
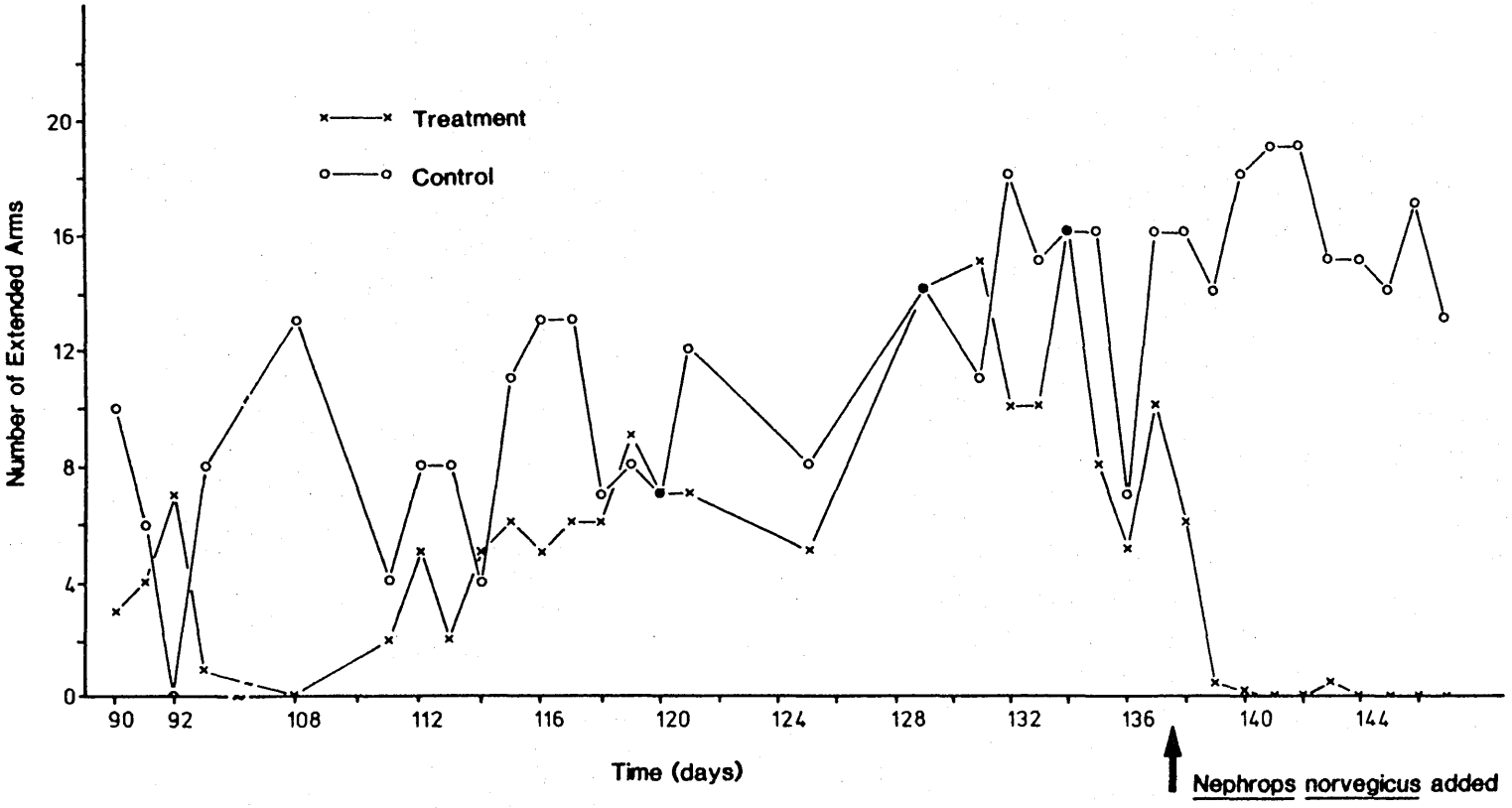


Figure 4.10 Change in the number of visible extended arms of Amphiura chiajei on the sediment surface in the control and treatment area (burrowed area).



number observed was 22 at the surface, of which 19 were extended. The average number of arms at the surface of the control tank was 16.8, a total of 3.36 arms per individual (under optimum conditions).

Generally, the activity of the A. chiajei increased over the time that the observations were made from mid-March to mid-July. This is more clearly observed in Figure 4.9, which shows the total number of arms at the surface, as there was less variation than in Fig. 10.

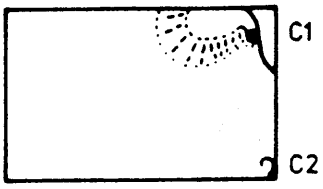
In the treatment tank one C. macandreae was established, present in its burrow when observations were begun. Prior to the addition of N. norvegicus, there was no significant difference in the total number of arms at the sediment surface, between the control and treatment tanks. However, there was a significant difference ($P < 0.05$) in the number of extended arms due to the presence of C. macandreae. Hence the presence of C. macandreae had some inhibitory effects on A. chiajei activity. After the N. norvegicus was added to the system, the difference in activity between control and treatment was highly significant ($P < 0.01$), the animal having a highly inhibitory effect in causing the A. chiajei to withdraw into the sediment.

4.3.4 Interaction of Burrowers with Surface-Visible Fauna

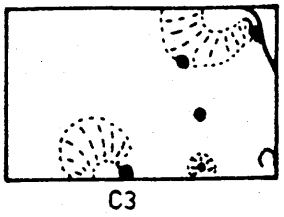
4.3.4.1 Development of Burrow Structure

Mapping of the two mesocosm tanks started shortly after the tanks were divided into two working areas each. The burrowers were added to each of the treatment areas on Day 33. The development of burrow structure and change in topography of the treatment areas along with chronology is shown in Figures 4.11 and 4.12. All the C. Macandreae in T4 burrowed down after a short period, each producing a spoil heap around its main entrance. The individual N. norvegicus in T5, after bulldozing the surface sediments of the treatment area for 48 hours, escaped into the control side of the tank. Over a period of 12 hours it twice more gained access to the control side and

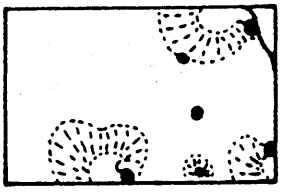
Figure 4.11 The development of the burrow of Calocaris macandreae in the experimental tank T4.



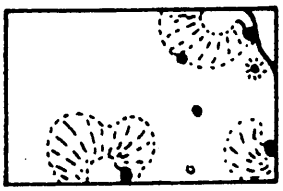
Day 37: Three Calocaris macandreae introduced. One burrows down top right (C1) corner with large sediment excavation pile. Second animal sits in scrape (C2)



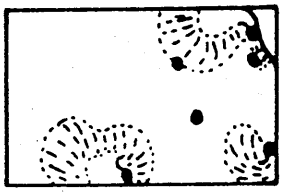
Day 43: C2 still in scrape. C1 has burrowed up with two exits. C3 has burrowed down with large excavation pile, middle bottom with one exit.



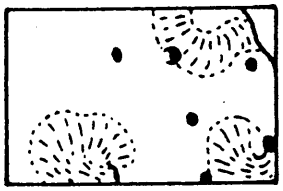
Day 46: No apparent change with C3 and C1. C2 has burrowed down with excavated sediment pile.



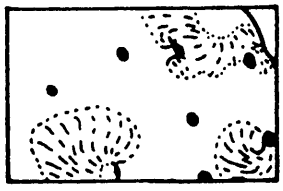
Day 51: C3 has closed off its main exit. Sediment pile for C2 is enlarged.



Day 55: C2 enlargens exit.



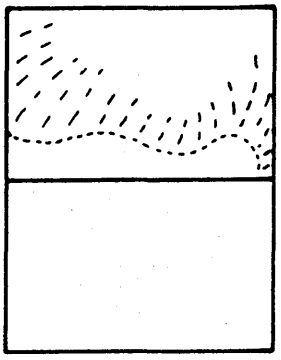
Day 58: New entrance appears, possible C1 or C3. C1 closes off main entrance. C3 closes off main entrance.



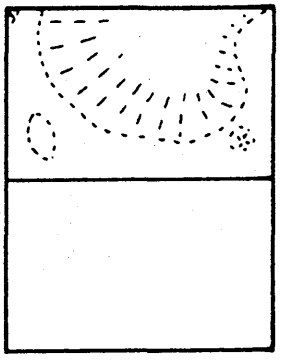
Day 73: Additional exit appears, possibly C1 or C3.

Shaft Main Entrance Excavated sediment pile

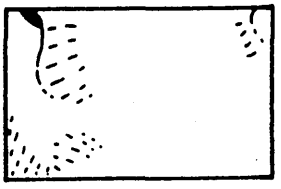
Figure 4.12 The development of the burrow of Nephrops norvegicus into the experimental sediment tank T5.



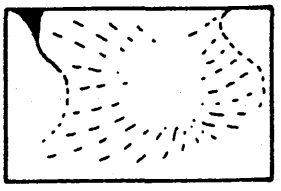
Day 37: Nephrops norvegicus introduced into tank. Bulldozes scrape down bottom side of tank piling sediment on top side.



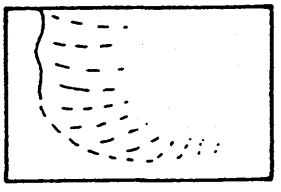
Day 43: Scrape develops. However animal accesses other side of tank (control area), keeps doing so until both sides equally surface disturbed. Animal left in new "treatment" side of tank (old control area).



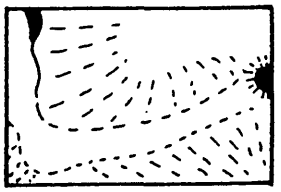
Day 46: Two scrapes bulldozed, main one undercutting sediment on top left hand side.



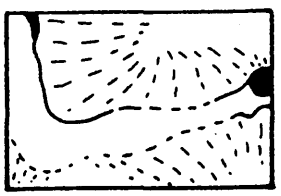
Day 51: Scrape develops. Sediment piled high in centre of tank. Animal burrows under top left hand side.



Day 55: Excavation pile develops. Animal fully under.



Day 58: Exit is opened up, with surface scrape joining entrance and exit. Sediment piled top middle and bottom right.



Day 73: Surface scrape and sedimentary piling more pronounced.

disturbed the sediment there. This original control area was then redesignated the treatment area and the original treatment area was designated the new control. Recovery was then monitored in the new control area. By Day 58, the N. norvegicus had completed a simple burrow with two openings.

4.3.4.2 Change in Abundance of Surface-Visible Infauna

Plates 4.1 to 4.4 with overlays show the sediment surface for each of the areas at the end of the experiment. The overlays highlight the major surface features and the presence of surface-visible infauna as observed under the microscope. A key to the infauna is given in Table 4.4 as is a note of the other species observed over the experimental period.

The change in abundance of the major, dominant, visible species is shown in Table 4.5 for T4 (C. macandreae) and Table 4.6 for T5 (N. norvegicus). The distribution of the majority of these species within the tanks was visibly aggregated even before they were divided. For example Turritella communis was dominant in the left hand side of T4, whilst no maldanids nor any individuals of Melinna palmata were identified in the right hand side. Corbula gibba was abundant in T4 and rare in T5. T. communis was rare in the left side of T5, whilst maldanids were more abundant there. Abundance of these animals did vary even before addition of the burrowers. T. communis browsing in surface sediments were often well camouflaged, whilst C. gibba would withdraw from the surface of the sediment if the tank was accidentally knocked.

Change in abundance and dispersion of these species is shown in Figures 4.13 to 4.17. In the plots of dispersion, the greater the value, the more aggregated the distribution of that species was. Amongst the plots,

Plate 4.1 Treatment area of Tank T4, burrowed by *Calocaris macandreae*.

Length of area approximately 40 cm.

Plate 4.2 Control area of Tank T4.

Length of area approximately 40 cm.

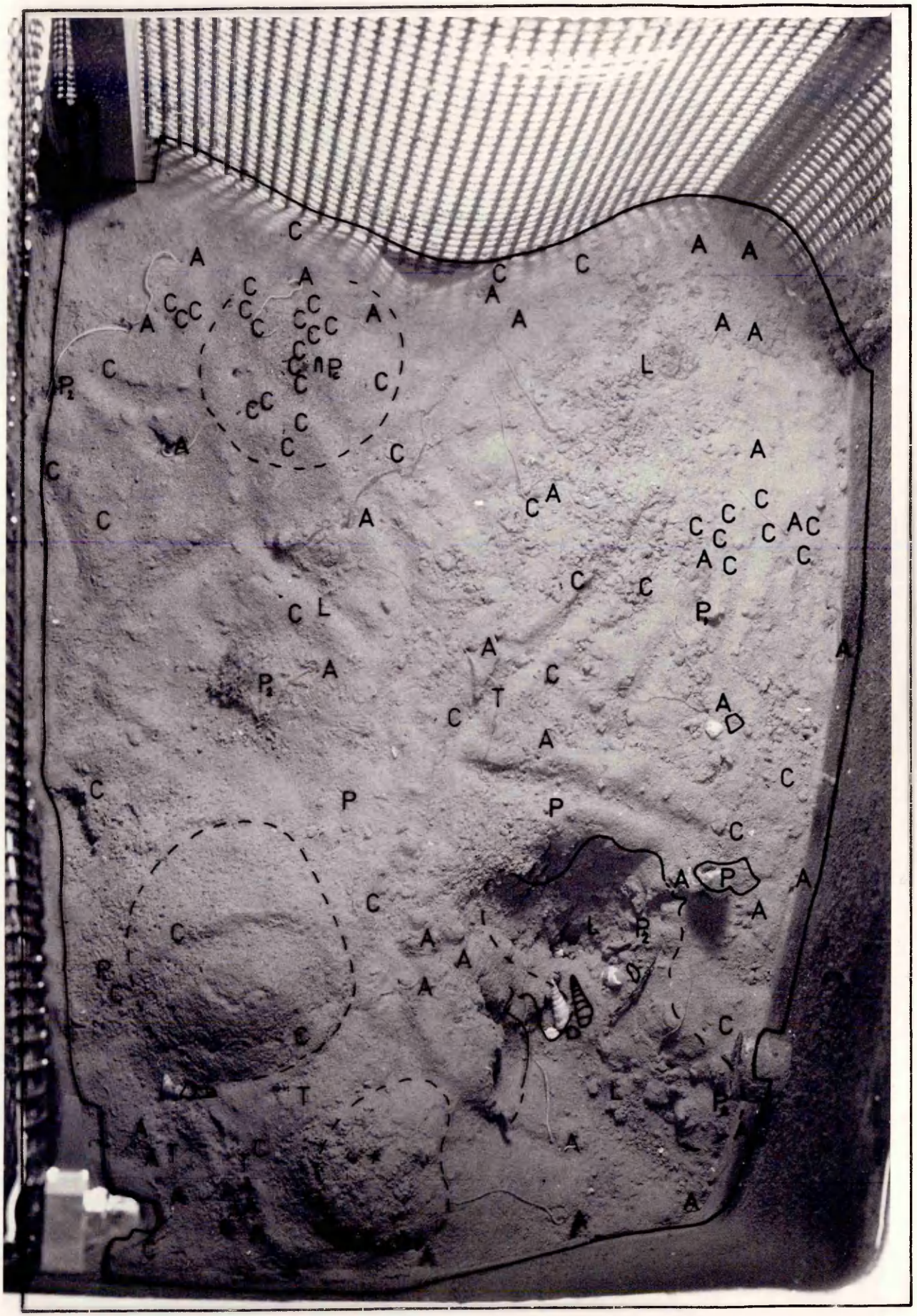

C
A
P
L
T
D

Plate 4.3 Control area of Tank T5.

Length of area approximately 40 cm.

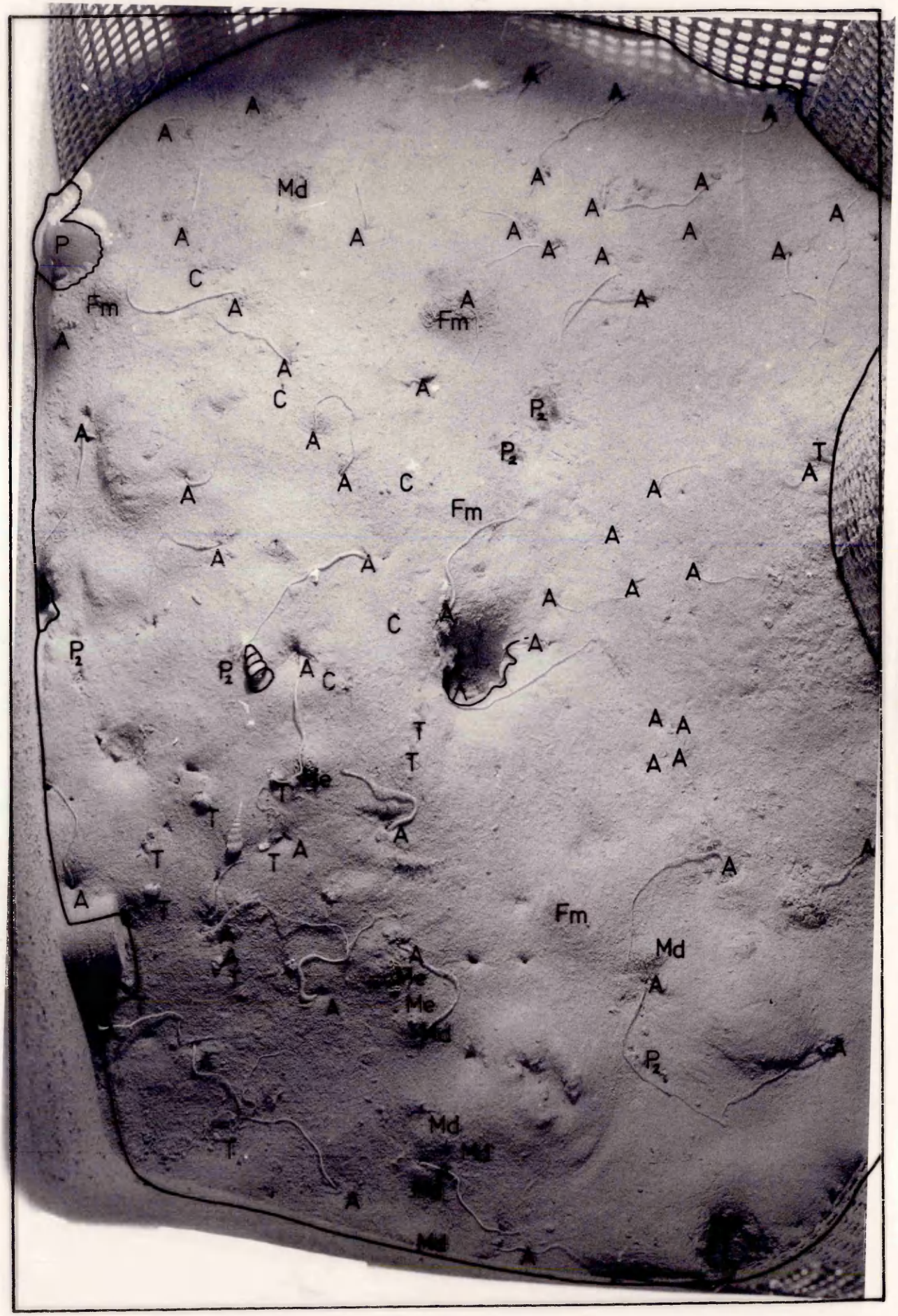

Md
P
Fm
C
Fm
P2
P2
T
Fm
P2
P1
C
T
T
T
T
A
Fm
Md
Me
Md
P2
Md

Plate 4.4 Treatment area of Tank T5, burrowed by Nephrops norvegicus.

Length of area approximately 40 cm.

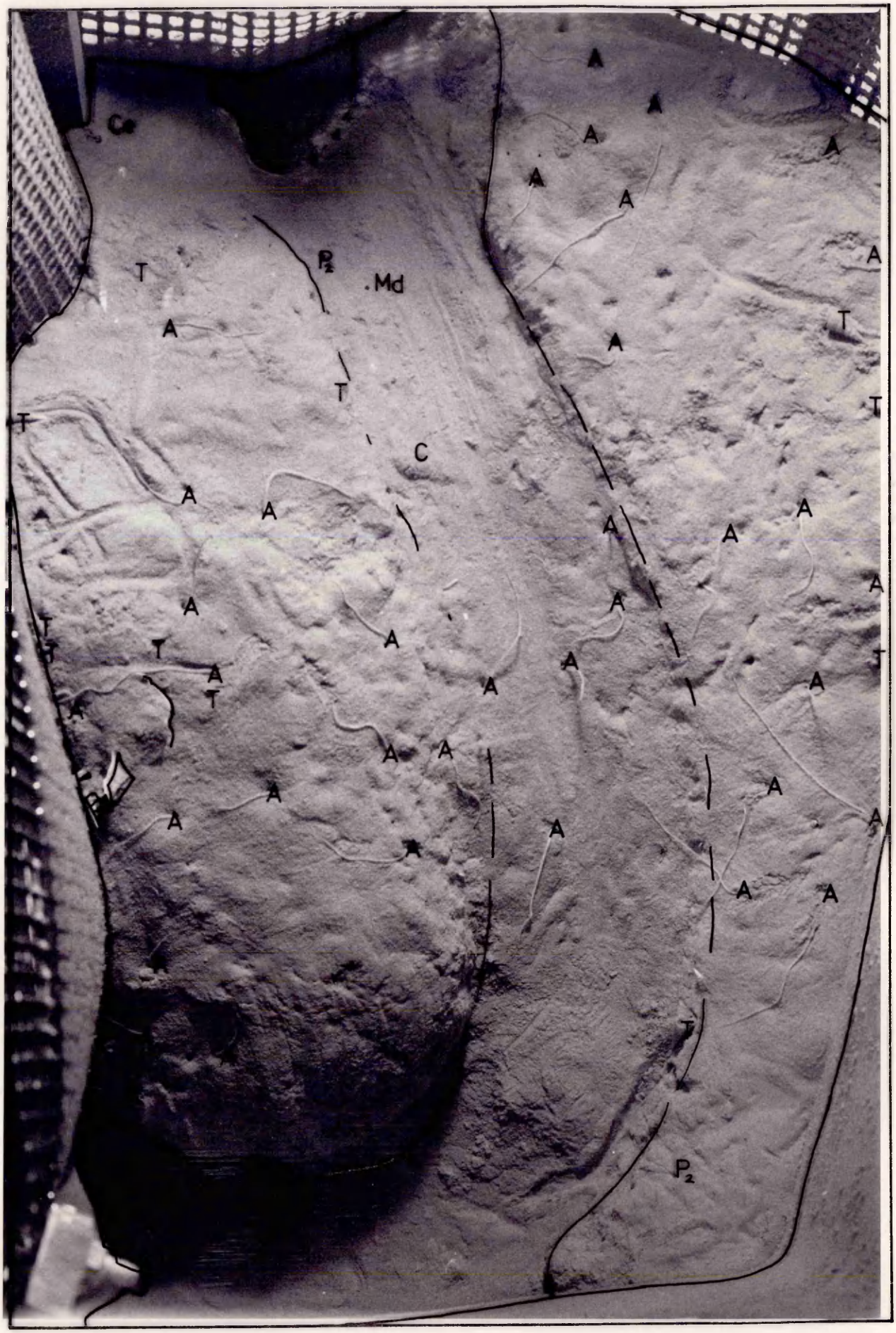

Co
P2
Md
C
P2

Table 4.4 Key to Distribution of Surface-Visible Infaunal Species.

A	:	Amphiura chiajei/filiformis
C	:	Corbula gibba
Ce	;	Cerianthid sp.
Fm	:	Faecal mound (polychaete)
L	:	Leptosynapta sp.
Md	:	Maldanidae sp.
Me	:	Melinna palmata
P	:	Pennatula phosphorea
P_1	:	Golfingia elongata
P_2	:	Cirratulus filiformis
	:	Shell fragment
	:	Shunted sediment or large polychaete mound
Pc	:	Pectinaria koreni
T	:	Turritella communis

Other Species Noted

Unknown bivalve siphons
Brachystoma eulimoides
Unknown Gastropod
Praxiella spp.
Magelona filiformis
Virgularia mirabilis
Allogromiid spp.
Hydroid spp.
Nematode sp.
Phoronis muelleri
Phascolion strombi
Ophiodromus flexuosus
Flabelligera affinis

Table 4.5 Change in abundance of dominant surface-visible species. T4 : *Calocaris macandreae*

	Day	*Corbula gibba*	*Amphiura* sp.	*Turritella communis*	*Golfingia elongata*	*Cirratulus filiformis*	Maldanidae spp.	*Melinna palmata*
CONTROL AREA	1	48	10	7	4	3		
	4	35	22	5	7			
	28	45	29	5	1	6		
	30	52	32	4	3	5		
	32	57	32	4	4	7		
	37	52	18	9	4	6		
	43	50	30	8	6	7		
	46	49	35	7	4	5		
	51	54	40	5	5	7		
	55	51	45	5	8	6		
	58	49	35	6	8	8		
	73	48	47	8	5	4		
TREATMENT AREA	1	21	18	75	1	3	1	
	4	25	28	75	2	1	1	
	28	34	22	83	2	9	1	1
	30	35	30	69		7	1	
	32	39	33	88		5	1	1
	37	33	28	86		4	1	
	43	39	27	86	1	8		
	46	39	28	75	2	5		
	51	42	34	77	1	7		
	55	44	43	85	1	9		
	58	40	36	76	3	7		
	73	37	33	72	1	9		

CALOCARIS MACANDREA ADDED

Table 4.6 Change in abundance of dominant visible species. T5 Nephrops norvegicus

	Day	Corbula gibba	Amphiura sp.	Turritella communis	Golfingia elongata	Cirratulus filiformis	Maldanidae spp.	Melinna palmata	
	1	3	21	31		5	2	1	
	4	1	26	28		3	1	1	
	28		51	26		5	3	1	
	30	1	65	20	1	6	2	2	
	32	2	53	23	1	3	2	2	
TREATMENT	37	2	54	21		6	3	1	
AREA	43		36	23		6	1	1	NEPHROPS ADDED
	46	1	46	18		5		1	
	51	1	48	19		3		1	
	55		48	18	1	2			
	58	2	38	17		1			
	73		37	12		2			
	1	5	33	6		3	8	3	
	4	6	24	6		2	10	3	
	28	5	33	9		3	6	3	
	30	5	53	8		5	8	5	
	32	5	52	8		5	6	5	
CONTROL	37	2	38	8		2	5	2	NEPHROPS ADDED THEN REMOVED
AREA	43	5	44	13		4	3	5	
	46	2	49	10		5	5	4	
	51	6	52	13		5	3	2	
	55	5	53	12		5	4	4	
	58	5	56	12		4	4	4	
	73	4	65	11		4	5	4	

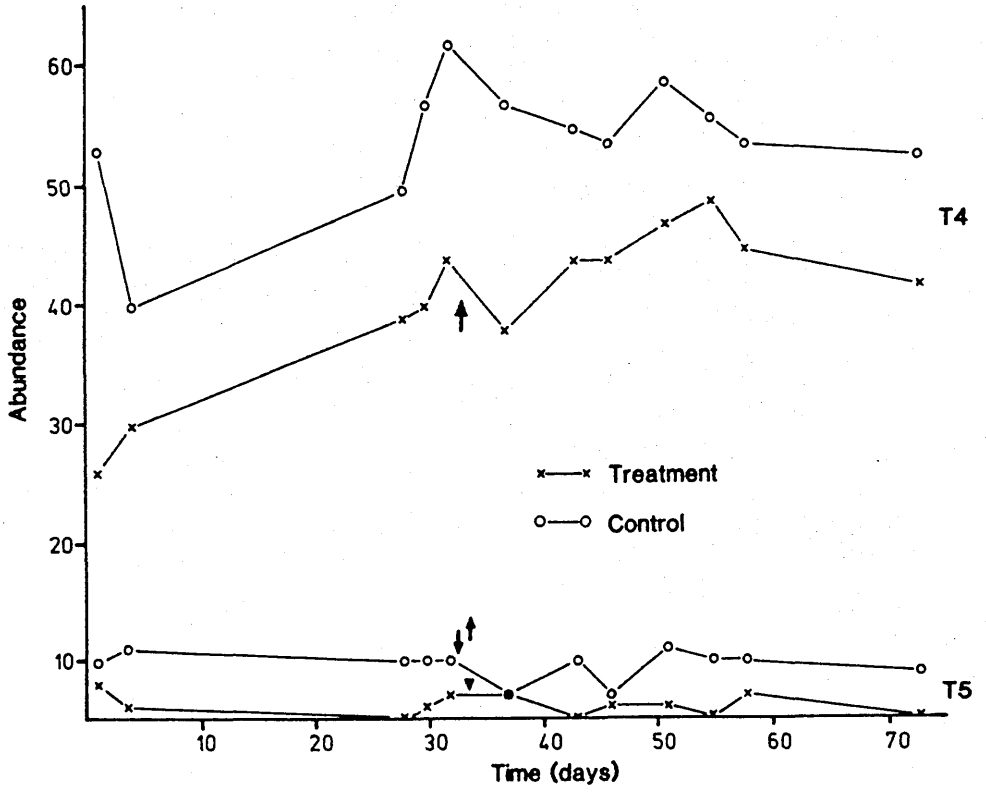
some effects were noted in both the areas of the tanks. This was due to the separation of the treatment and control areas by a mesh panel only.

Figure 4.13 shows the change in abundance of Corbula gibba and the change in relative dispersion of that species. A similar trend is shown by C. gibba in both areas from T4; an overall increase in visible abundance with a small momentary decrease when the C. macandreae were added. The numbers in T5 were much lower, and were fairly constant throughout the experimental period, with minor variation in the control area when the N. norvegicus was added for 48 hours, after which numbers returned to pre-addition levels. The dispersion of C. gibba (as given by the chi-squared value) in the burrowed area increased generally before levelling out, after the addition of the C. macandreae. The dispersion of C. gibba similarly increased in the unburrowed area, but dropped down to previous levels 28 days after addition of the burrower to the adjoining area, when most active burrowing had finished.

Changes in number of arms visible of Amphiura spp. are shown in Figure 4.14. There was a similar trend in this change in number in T4 with an overall increase in number visible with some variation. This variation was characterized by a decrease in the number visible in both areas, related to the addition of C. macandreae. It lasted approximately 5 days in the control area and 10 days in the treatment area. There was some departure at the end of the experimental period with a decrease in number in the treatment area. An overall increase in the number of arms visible was demonstrated by the Amphiura spp. in the control area of T5, although a large decrease occurred when the N. norvegicus was added for a short period. When the N. norvegicus was removed, the number of arms visible increased again. In the treatment area the number visible increased until the N. norvegicus was added. The number then decreased to half that visible in the control area.

Figure 4.13

Change in abundance of Corbula gibba after addition of burrowers to the experimental aquaria:T4 Calocaris macandreae, T5 Nephrops norvegicus. Arrows directed onto the plots refer to the addition of a burrower, away from refers to the removal of a burrower.



Change in relative dispersion (Chi^2) of Corbula gibba in T4 after addition of Calocaris macandreae.

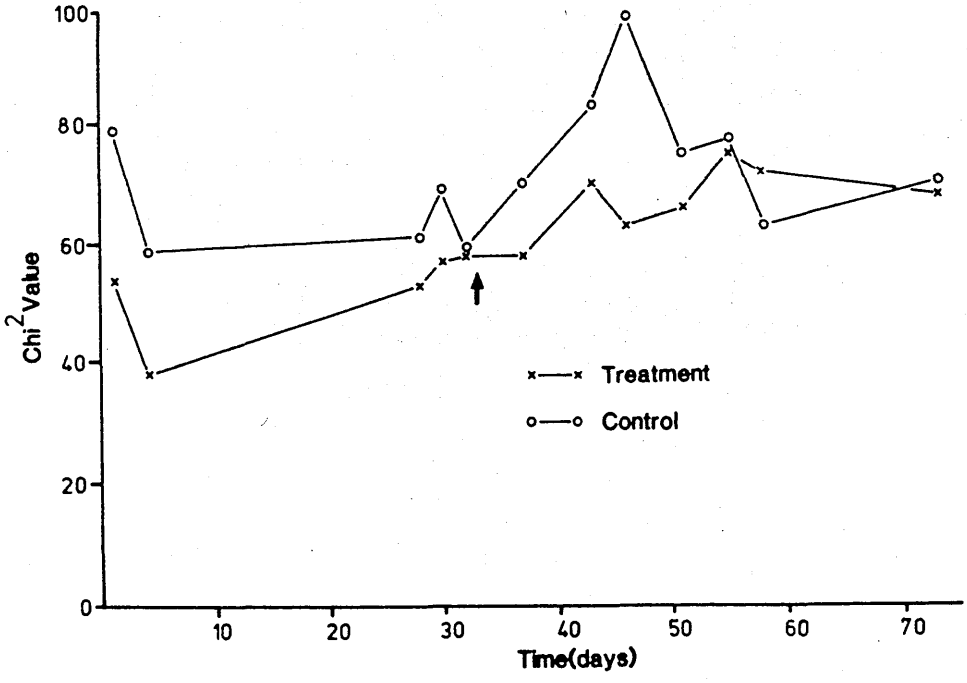
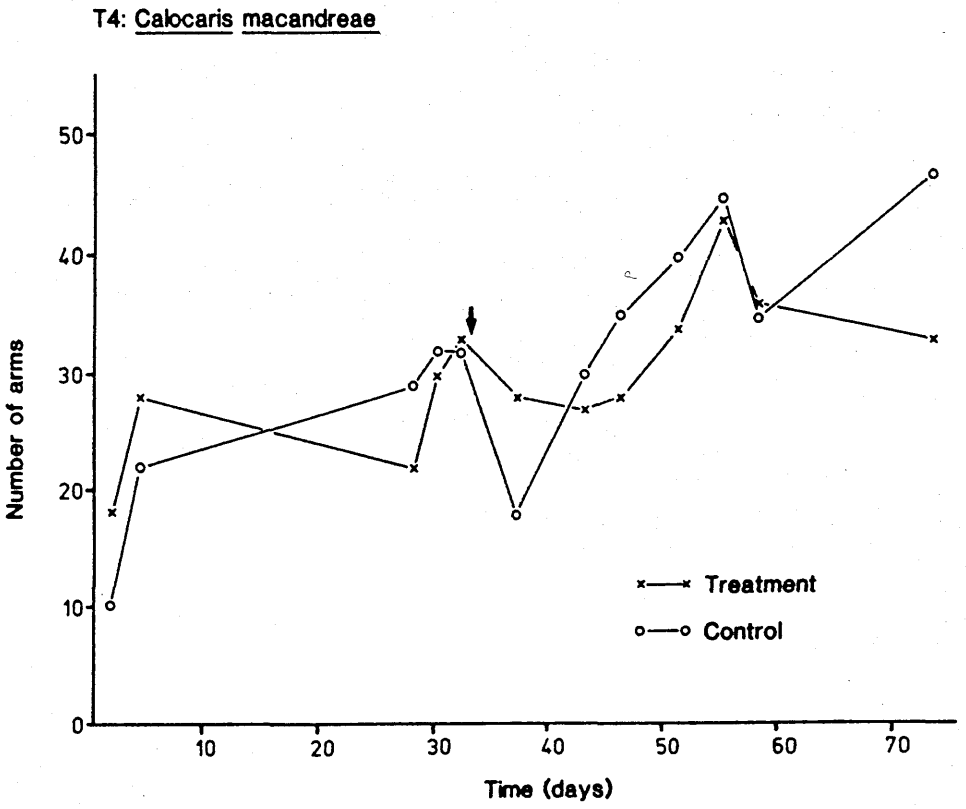
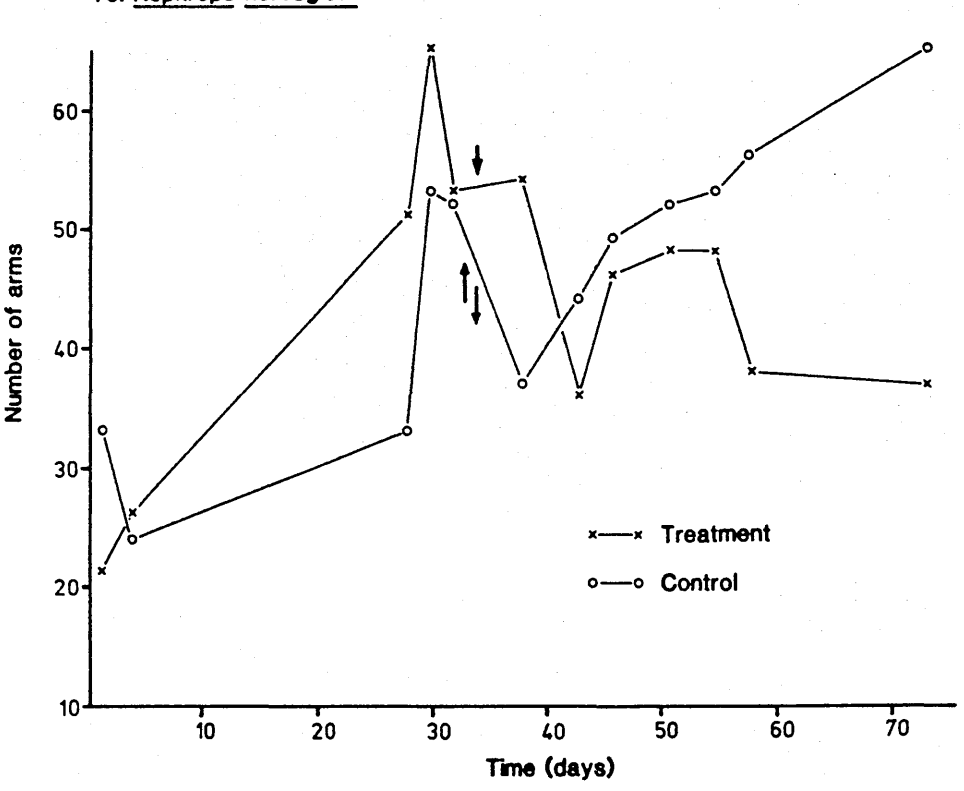


Figure 4.14 Change in the number of Amphiura spp. arms after the addition of burrowers to the experimental aquaria. Arrows directed onto the plots refer to the addition of a burrower, away, refers to the removal of a burrower





The change in dispersion of Amphiura spp. arms was shown for both tanks in Figure 4.15. In T4, there was an increase in aggregation following the addition of C. macandreae, followed by a return to status quo after 20 days. In T5, addition of N. norvegicus to the treatment area may have caused a decrease in the degree of aggregation for a similar period.

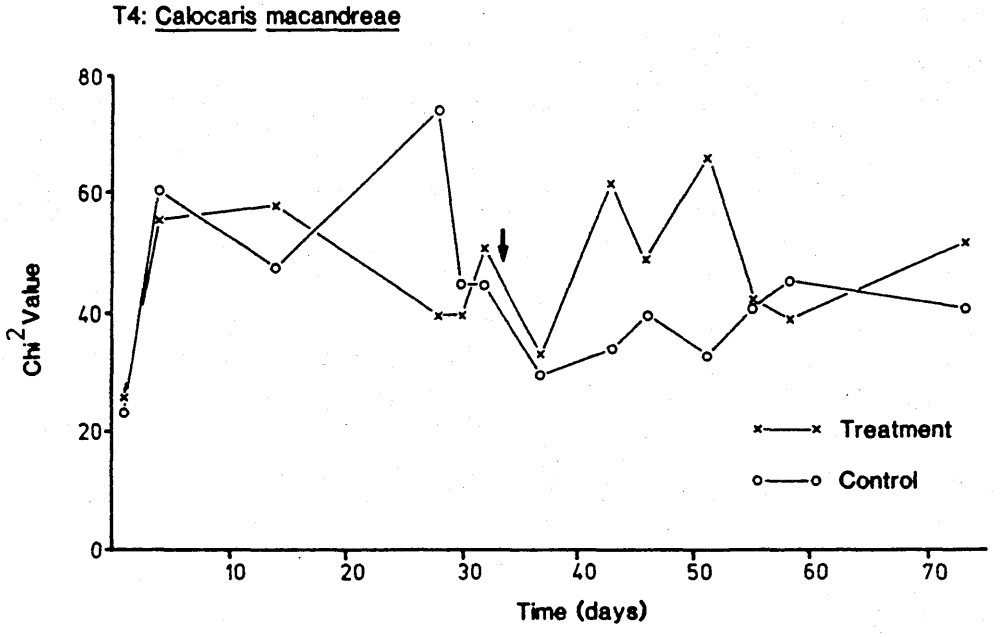
No effect of C. macandreae was demonstrated on the abundance of Turritella communis (Figure 4.16), which was constant throughout the experiment. N. norvegicus caused some effect in T5, as the abundance of T. communis decreased slightly in the burrowed area whilst it increased slightly in the control area. The degree of dispersion of T. communis (Figure 4.17) was constant except for some fluctuation in both areas of T4 and T5 when the burrowers were added.

The control area of T5 was still physically affected after removal of N. norvegicus from that area, as light silt put into suspension by the animals' activity in the treatment area settled out. The surface texture in Plate 4.3 was quite different from the C. macandreae control area shown in Plate 4.2.

4.3.4.3 Species Redistribution

The actual distribution of the dominant species in relation to the presence of a burrow belonging to C. macandreae, is shown in Figure 4.18. The boxes on the left hand side represent the distribution of these species in the treatment half of the tank at the start of the experiment, Day 1. The boxes on the right hand side refer to their distribution when the last observations were made on Day 73. The top box on each column shows the major surface features; prior to addition of C. macandreae just one large polychaete faecal mound was present whilst afterwards, burrow openings and spoil heaps were evident. Turritella communis were mainly aggregated around the polychaete faecal mound at the beginning of the experiment, but towards the end had aggregated more around one of the C. macandreae spoil

Figure 4.15 Change in the relative dispersion (Chi^2 value) of Amphiura spp. arms, visible in the experimental aquaria on the addition of burrowers. Arrows directed onto the plots refer to the addition of a burrower, away, refers to the removal of a burrower



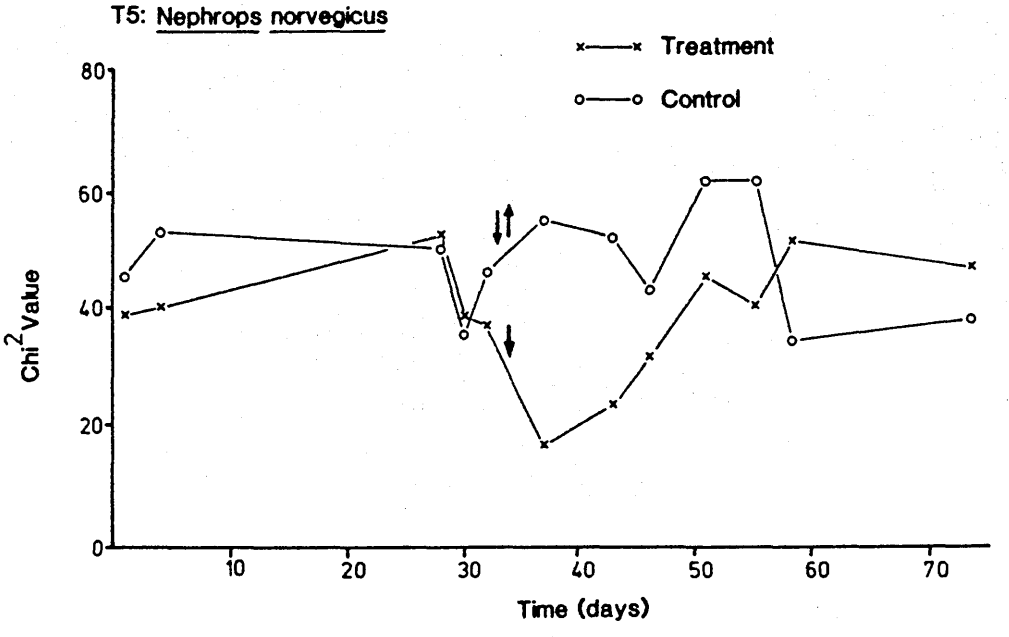


Figure 4.16 Change in the abundance of Turritella communis in the experimental aquaria on the addition of burrowers. Arrows directed onto the plots refer to the addition of a burrower, away, refers to the removal of a burrower.

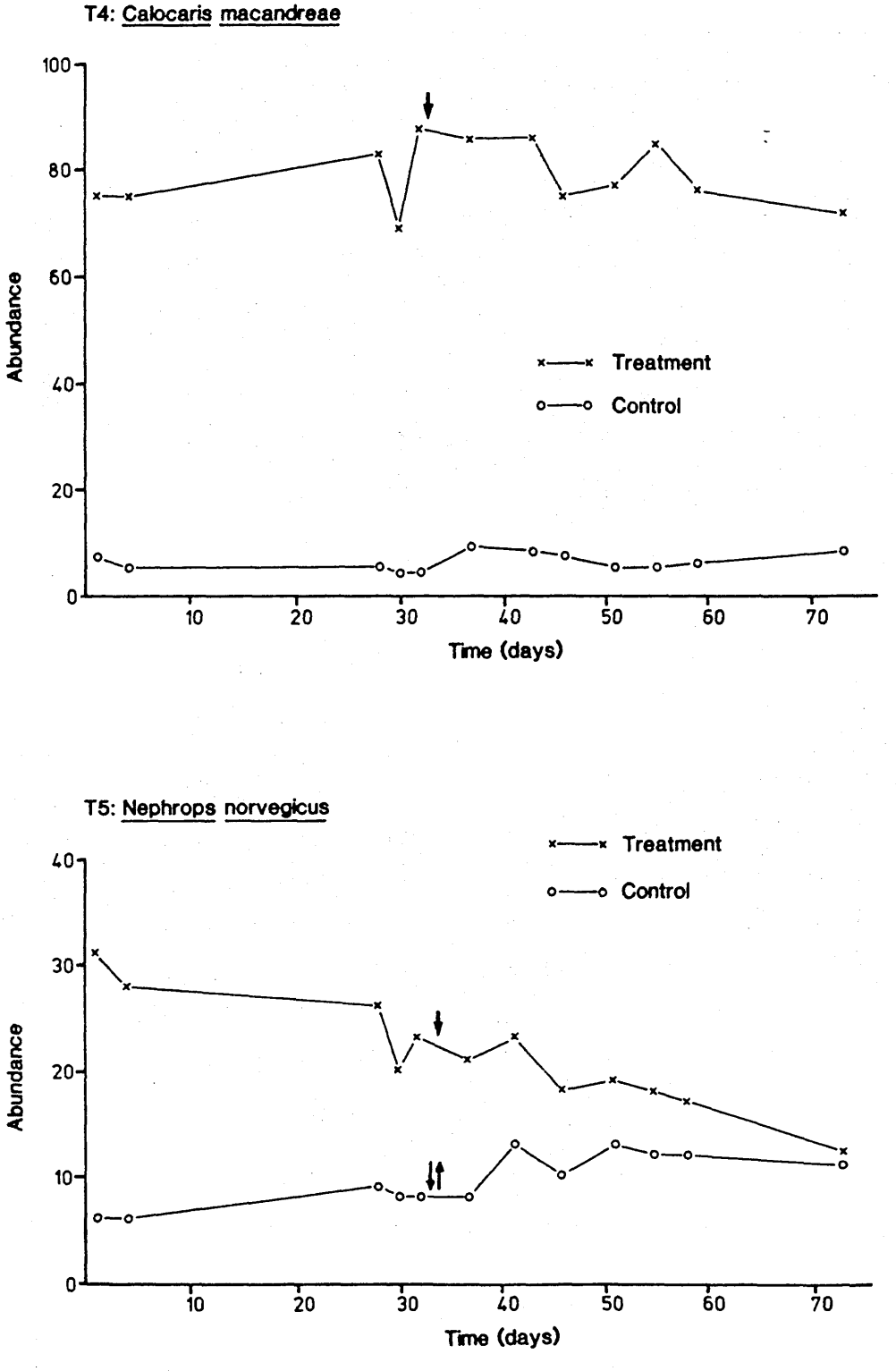


Figure 4.17 Change in the relative dispersion of Turritella communis in the experimental aquaria on the addition of burrowers. Arrows directed onto the plots refer to the addition of a burrower, away, refers to the removal of a burrower

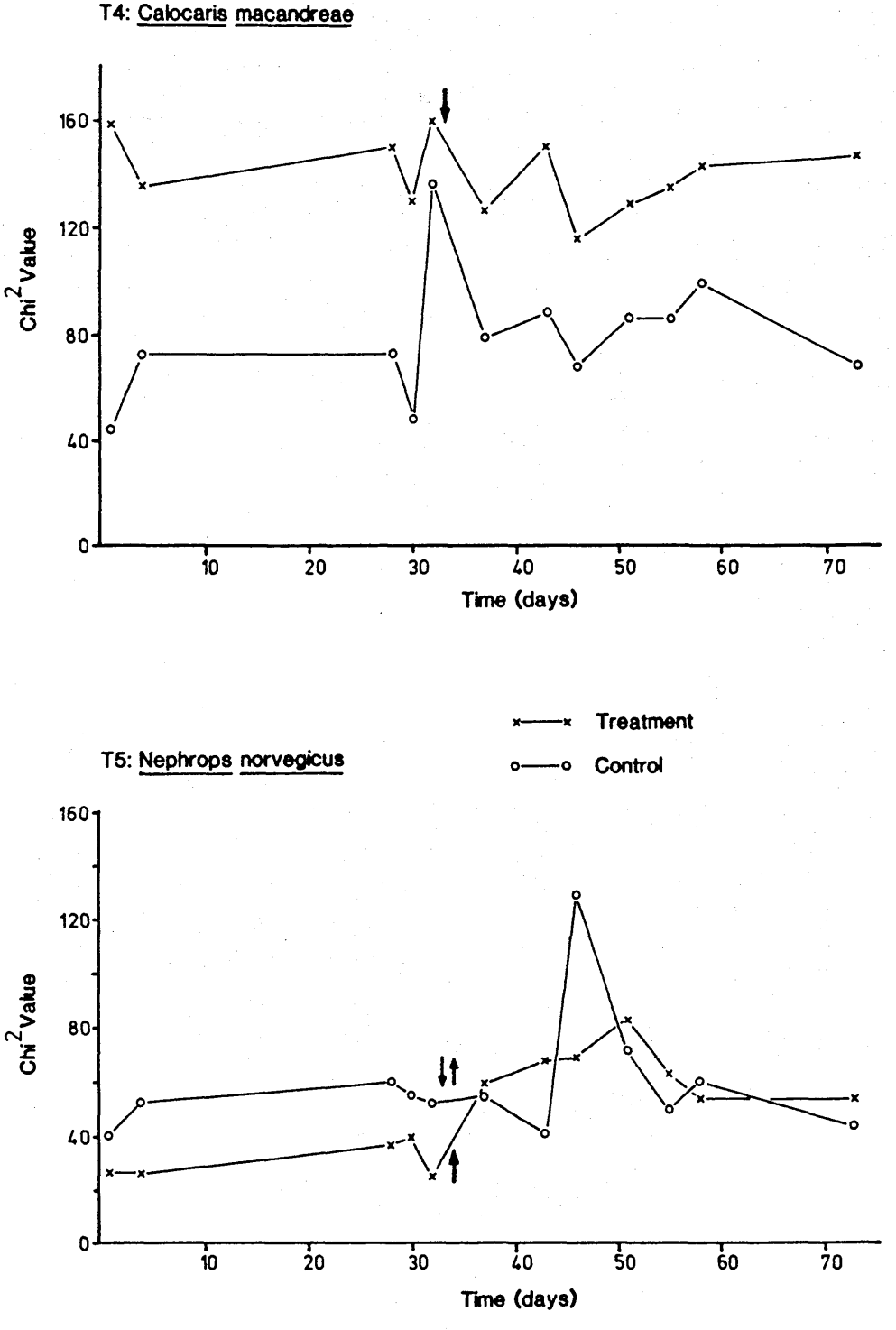
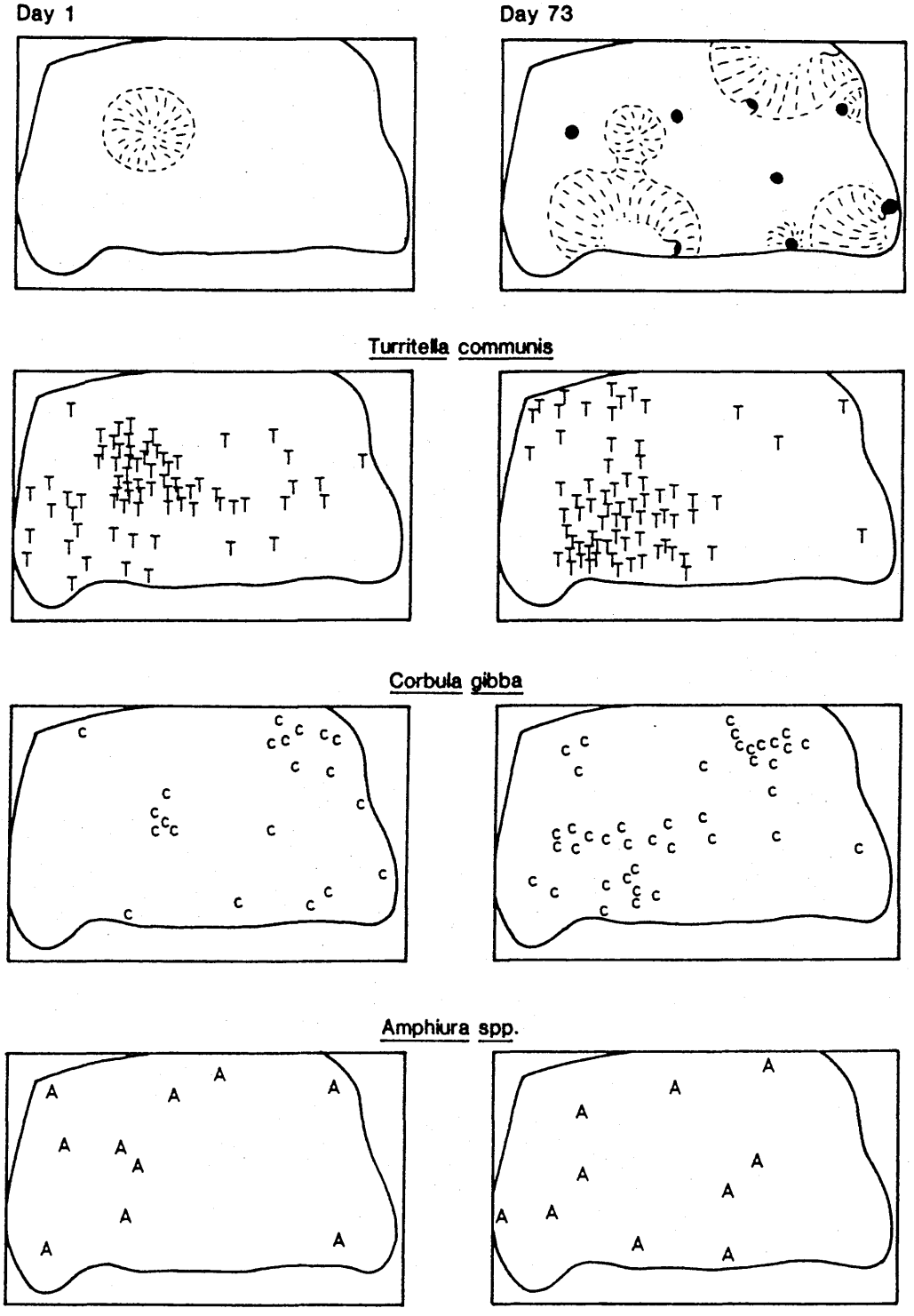


Figure 4.18 The distribution of dominant surface-visible infaunal species around tank T4, before and after the addition of Calocaris macandreae



heaps. This was also somewhat true for C. gibba which were observed to be orientated around spoil heaps. There was a noted lack of presence of C. gibba in the well burrowed bottom right corner. Amphiura spp. were seemingly not affected, and there was no obvious pattern to their redistribution.

The redistribution of dominant species in the treatment area of T5 is shown in a similar fashion in Figure 4.19. T. communis were reduced in number and shunted out from the main scrape onto the banked up sides of the sediment surface. Amphiura spp. were seemingly unaffected. Although none were centred in the middle of the scrape, some were positioned close on the banks and were seen to push some arms out into the scrape. The number of Amphiura spp. remained seemingly unchanged. The polychaete Cirratulus filiformis was reduced in number and remained near the edge of the mesocosm tank.

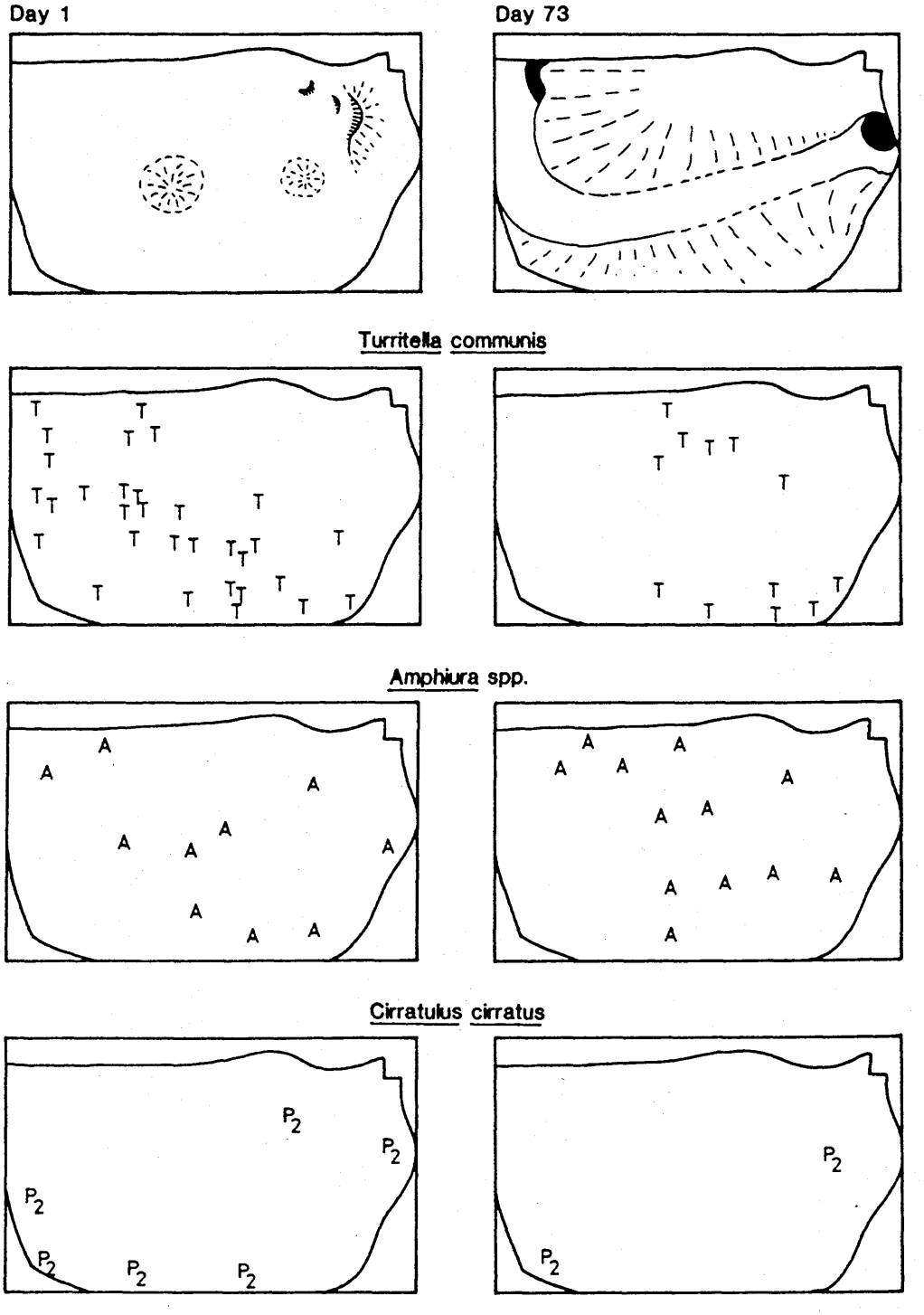
4.4 DISCUSSION

The mesocosms described in this experiment were restricted somewhat in terms of environmental simulation. Faunal levels had dropped from natural levels (established in Chapter 2) and exclusions had occurred, for example, epifaunal predators were not included and, because of the selectivity of the grab used, infauna which occurred deeper than approximately 10 cm were absent. However, the experiments were successful in so far as the effects of burrowers were observed in an interactive system and at a level that still matched, to a great extent, the natural environment.

4.4.1 Burrower/Community Interactions

Overall, it was concluded that the burrowers had an inhibitive effect on the mesocosm community structure, although both crustaceans also caused a degree of enhancement. There was a general depletion at community and

Figure 4.19 The distribution of dominant surface-visible infaunal species around tank T5, before and after the addition of Nephrops norvegicus.



species level with a shift in community composition in the burrowed areas. The greatest interactive effect was noted in the area burrowed by N. norvegicus. The area burrowed by C. macandreae represented an intermediate stage between this and the control area.

The number of post-experimental replicate samples from each area was restricted through processing time to 3 from each sector. This was compared with the 6 replicate (2 from each sector) pre-experimental cores taken to establish the mesocosm tank fauna. Because of the contagious distribution and variable abundance of species this led to some difficulty in statistical comparison of the presence and absence of some species in the different sectors. However, in terms of community statistics (species number, abundance, etc.), variation was such that the small number of replicate cores were fairly representative.

In common with the results from Chapter 3, Foraminifera were again the most abundant fauna, in particular the agglutinating multilocular Type 3. this species presented a problem in that it is difficult to differentiate between living and dead individuals. This problem has been previously highlighted by, amongst others, Hoglund (1947) and Gooday (1986). The criteria used to identify living individuals was based on the presence of an intact test and some stained protoplasm. However, the test content was not always clear and so a small amount of the abundance observed may have been of recently dead animals. The abundance of Foraminifera was seemingly unaffected by either of the treatments which may have been due in some part to this inability to differentiate between recently dead and living specimens. Thomas & Davidson (1962) recorded the presence of Foraminifera in the foreguts of N. norvegicus. They suggested that only the very large individuals were preyed upon directly and that most were secondary food items in the guts of other prey. Bailey et al. (1986), however, found only a very low incidence, which suggests that they are not a preferred prey.

Within the area burrowed by N. norvegicus there was a noted decrease in species number, biomass and size ratio. The latter indicated that the average size of individuals in this area was much smaller. The decrease in biomass was due to the absence of gastropods, in particular T. communis. Absence of gastropods then resulted in the relative dominance of polychaetes in the percentage species composition. Shells of T. communis were present in the burrowed area, a number with decaying tissue present, which indicated recent mortality. Live individuals had been present in this area in the pre-experimental cores. Absence of T. communis and evidence of mortality from this area agreed with evidence from Chapter 3, where its abundance was much lower around the burrow of N. norvegicus. It was previously thought that this species would be resilient to disturbance because of its hard shell and life mode. Yonge (1946b) noted this species to be a deposit/suspension feeder using ciliary action. It lies buried at the sediment surface with an opened inhalent and exhalent channel at the mouth for respiration and feeding. Pearson (1971) also observed this deposit/suspension feeding mode. Using either method its ciliary action may be susceptible to clogging by fine sediments. It was observed that N. norvegicus ventilatory and burrowing action could suspend a large amount of fine sediment which made the water column quite turbid. Natural currents were replaced by a flow through system in the mesocosm which could not always prevent the build up of turbidity. High sediment loading could, therefore, have been responsible for the T. communis mortality. Aller & Dodge (1974) and Murphy (1985) have found evidence that Callianassa spp. can affect fauna and flora subtidally through resuspension of particles rather than strictly via sediment disruption.

Amphiura chiajei and Corbula gibba, two other species that can have significant biomass, were also absent from this area. Possible reasons are discussed in Section 4.4.3.

There was no significant difference in abundance nor in abundance ratio (average number of individuals per species) in the area burrowed by N. norvegicus. This was due to a shift in community composition in that area, from a heterogeneous mix of species to a community dominated by oligochaetes and nematodes: this was evident from the decrease in size ratio. This shift was also noted in the K-dominance curves, which indicated a low diversity and a high degree of dominance. Bonsdorff (1980, 1983) found tubificid oligochaetes to be one of the dominant pioneer species in colonizing disturbed areas after dredging. This disturbance was a single phenomena and not continual. In contrast, no significant pattern of distribution of oligochaetes was observed by Posey (1986) in response to the continual bioturbatory activity of Callianassa californiensis. Brenchley (1981) also found no significant difference in numbers of oligochaetes and nematodes in areas bioturbated by the sand dollar Dendraster excentricus. Nematodes, like oligochaetes, are quick to colonize disturbed areas (Sherman & Coul, 1980). Bell et al. (1978) found that the density of nematodes increased around the burrows of Uca pugnax (fiddler crab), postulating that this was due to: (1) a decrease in the number of copepods or (2) an increase in faecal pellets and associated microbial activity. From his review on disturbance, Probert (1984) also noted in a meiofaunal response that as high abundance of nematodes could utilize enhanced microbial activity from faecal mounds and the turn over of deeper organic rich sediments. He also noted that, in the absence of competitors, opportunistic species could exploit new habitat patches. Rhoads & Boyer (1982) suggested that under normal conditions opportunistic pioneering species are excluded from equilibrium assemblages by competitive exclusions such as trophic group amensalism (Rhoads & Young, 1970). Thayer (1979) described the reason for this exclusion as "bulldozing". However, when bulldozing reaches a level where the equilibrium community is upset, exclusion may be negated. The bioturbatory activities of Callianassa californiensis and

Dendraster excentricus mentioned above may have been insufficient to upset their equilibrium communities.

For a species to increase in abundance, it must take over the niche of another species or extend the size of its own in response to an increasing resource. It is suggested that both these factors contributed to the increase in nematode and oligochaete abundance in response to organically rich sediments and lack of competition from less resilient species.

Of the three dominant polychaetes, ~~Paronis~~ Levinsenia gracilis and Paradoneis lyra appeared in greater abundance after the experiment. Individuals of these species were often very small with thoracic width less than 0.5 mm. It was thought that they had settled out during the course of the experiment and that juveniles of P. lyra were not tolerant of the bioturbation of N. norvegicus. No effect was observed on Magelona filiformis nor P. gracilis. This was in contrast to the results in Chapter 3 and from the literature, where reductions due to bioturbation have been demonstrated in tubiculous spionid polychaetous assemblages (Flint & Kalke, 1986; Brenchley, 1981). M. filiformis is spioniform but does not possess a distinct tube as it is a discretely motile burrower (Fauchald & Jumars, 1979). It is suggested that because the N. norvegicus did not actually burrow under and produce a "normal" sub-surface burrow, activity of these two polychaetes remained largely unaffected.

The community structure of the area burrowed by C. macandreae was not as adversely affected as that of the area burrowed by N. norvegicus. The disturbance was not of the same nature and resulted in a different end community. The diversity of this area was similar to that of the control area and species number remained unchanged from the beginning of the experiment. Abundance was slightly higher, but a decrease in biomass was observed. This decrease was again associated with a general decrease in molluscan

abundance, principally Turritella communis and echinoderm abundance, notably Amphiura filiformis. Owing to these decreases, the community structure seemed to represent an intermediate stage between the control area and the area burrowed by N. norvegicus. However, an important difference was the increase in abundance of the polychaetes Exogene sp., M. filiformis and L. gracilis in this area. It was thought that like Paradoneis lyra, Exogene sp. had settled out through the open circulation aquarium system over the experimental period. Increase in abundance of the polychaetes could be due to two reasons: (1) migration from the area burrowed by N. norvegicus in response to the large scale disturbance there, or (2) migration into the area in response to a favourable resource provided by C. macandreae. Levin (1982) has previously described emigration of spionid polychaetes in response to stress, and emigration of the amphipod Rhepoxynius abronius and the polychaete Nephtys caeca has been observed by Ambrose (1984b) in response to the presence of invertebrate predators. It is possible that the motile polychaetes found here were migrating away from the continuous surface activity of N. norvegicus, to the nearest refuge. It is also likely that the organically rich excavations of C. macandreae provided an attractive food resource for the surface deposit feeders, M. filiformis and P. gracilis.

4.4.2 Burrower/Redox Potential Interactions

The redox potential of a separate experimental mesocosm indicated that these tanks were consistently well oxygenated to 25 cm depth. Deep occurrence of the RPD layer, indicating deep oxygenation, has been associated with high-order successional assemblages by Rhoads & Boyer (1982). They suggested that this was maintained by the infaunal mediated bioturbatory processes of vertical particle mixing and pore water exchange by respiratory pumping. The addition of N. norvegicus led, surprisingly, to the formation of an RPD layer at approximately 5 cm sediment depth. Previously, from field

studies, megafaunal bioturbators, for example, the enteropneust described by Flint & Kalke (1986) have lowered the RPD layer. Three possibilities are suggested to explain the RPD layer formation: (1) compaction by N. norvegicus, (2) burial of organic matter within the burrow of N. norvegicus and (3) burrowing by N. norvegicus inhibited deep macrofaunal bioturbation.

It is possible, but thought unlikely, that compaction through bulldozing and trampling was the major factor responsible. Firstly, it would occur mostly in the burrow and its approaches; this was not evident from the distribution of the profiles. Secondly, compaction would occur over a period of time, as sediments are gradually bulldozed and a gradual development of the RPD layer would be expected. However, the RPD layer developed relatively quickly. Thirdly, the RPD layer only formed after the animal burrowed, 10 days after the initial bulldozing.

N. norvegicus had previously been observed in a glass walled tank burying food material (organic matter). This always occurred in the deepest central part of the burrow and this would only have caused a localized effect, not the general RPD formation observed.

The most likely explanation for RPD layer formation in the mesocosm tank (although neither of the above suggestions are totally ruled out) is the inhibition of macrofaunal activity, which would prevent general sediment aeration. This is supported by the previously suggested emigration of species and by the general decrease in faunal abundance in the N. norvegicus burrowed area.

4.4.3 Burrower/Surface-Visible Infauna Interactions

During the experimental period that the Amphiura chiajei were maintained in defaunated sediment, only one individual was ever observed at the sediment surface. The individual was moving across the surface and as the observer's shadow fell across it, it stopped and buried itself. An individual

C. macandreae was present in the tank but this was in its burrow where it appeared to be passive. The ophiuroid did not appear to have spawned as the water column was clear of gonadal products. It is not known what the animal was responding to. Woodley (1975) notes that amphiuroids are only found on the surface in response to some upheaval of the substratum or during spawning. Previously in the mesocosm tanks, individuals were observed on the sediment surface during an epidemic spawning. This was triggered by enclosing the mesocosm tank in a black polythene tent during the day. It occurred simultaneously in three separate tanks. Individuals rose out of the sediment on extended limbs with oral disc some 3-5 cm above the sediment surface. Both males and females spawned, eggs dropping slowly to the sediment from the oral disc whilst sperm clouded the water. When spent each animal sank back down into the sediment, the process lasting approximately 5 minutes each, as reported by Woodley (1975) and some 30 minutes for total cessation of spawning activity. Some arms were then observed to gather in eggs from the sediment surface, but it is not known whether this was for feeding or brooding purposes. Similar spawning behaviour has been observed individually by Woodley (1975) and epidemically by Okelmann & Muus (1978). Buchanan (1964) reported a rapid mortality after breeding but this was not substantiated here, and the populations in the mesocosm tanks remained healthy.

An overall inhibitory effect was demonstrated by megafaunal burrowers on A. chiajei, Thrush (1986) found that surface disturbance by simulated crab pit digging also had a significant inhibitory effect on the amphiuroid Amphipholis squamata. In this study the nature of the effects of the two burrowers were, however, different. C. macandreae caused an increased amount of individual movement. This was identified as being in response to a number of separate effects. Movement away from active burrowing perturbation, movement towards excavated organic rich sediment and, finally,

movement down towards the aerated sediment associated with the main C. macandreae burrow galleries. Okelmann & Muus (1978) report A. chiajei as a sediment perturbator itself, excavating galleries at about 3 cm sediment depth, where it was mostly situated in this experiment.

The general activity of A. chiajei increased in the control area over the experimental period. This was associated with the spring phytoplankton bloom which occurs consistently between late February and early May (pers. comm., K. Jones), when this experiment took place.

The only effect exhibited by the activity of C. macandreae on A. chiajei was on the number of extended arms at the sediment surface. In contrast, N. norvegicus activity had a highly significant effect on the activity of A. chiajei. Two individuals disappeared entirely, presumably killed by the crustacean. It had been held for some time previous to addition and, although fed occasionally, may have been in need of further feeding. Although not a common dietary component, amphiuroids have been found in the stomachs of N. norvegicus (Oakley, 1979). Remaining individuals completely withdrew into the sediment. Occasionally an arm was ventured at the sediment surface, presumably for burrow ventilation, a function ascribed to the arms by Woodley (1975).

In the control tank an average of 3.36 arms were noted per individual over the experimental period. Okelmann & Muus (1978) also described amphiuroid activity by this method before and after feeding. A. chiajei had 2.1 and 2.67 arms protruding respectively, whilst A. filiformis had 3.07 and 3.77. These differences were ascribed to the differing feeding habits of the two species. A. filiformis holds its arms up in the water column suspension feeding and A. chiajei uses its arms on the sediment surface to deposit feed. The increased average number of arms of A. chiajei in this study is postulated to be a population characteristic dependent on local food conditions.

In the mesocosm tanks, under close observation, a diverse fauna was visible. Unfortunately, no obvious difference could be discerned between A. chiajei and A. filiformis. Separation could theoretically be made by their feeding modes as described above and the fact that A. filiformis aggregates closer (Buchanan, 1964; Warner, 1975). However, A. chiajei will also on occasion lift arms into the water column to ventilate their burrows. Hence no differentiation was made between the species.

The dispersion of the visible species was contagious which agrees with the macrofaunal core data. In a number of cases species were distributed about other species. For example, a number of Turritella communis were observed to be distributed around the large faecal mound of an unidentified polychaete in T4 before addition of C. macandreae. Corbula gibba were also noted clustered around the faecal mound of an individual Pectinaria koreni. This mound was present in the same area for over 12 months. It was composed of larger grained sediment than in the surrounding area. At times a sediment flume was observed ejected from a small tube at the top of the mound. Heavier grains fell onto the mound whilst finer grains remained in suspension for a longer period. Sediment processing and life style of the related species P. gouldii has been reviewed and described by Busch & Loveland (1975). They note similarly that sediment is ejected from the posterior tube aperture extending slightly above the sediment surface and is deposited in graded mounds of faecal rich substrate. Fauchald & Jumars (1979) reviewed feeding in the pectinarids and postulated that U shaped burrows were formed semi-permanently in nutrient rich, oxygen poor, fine grained sediments. Evidence was visible of a second shaft or cave-in of deep excavated galleries, by a depression in the sediment surface adjacent to the faecal mound (the P. koreni burrow can be seen in the upper left corner of Plate 4.2 and is circled with a broken line in the overlay).

Prior to addition of burrowers, there was a general increase in the emergence of species. At the beginning of the experiment, the dividing panels were pushed into the tanks. This caused some disturbance as the mesh supports had in some cases to be hammered in. Sediment adjacent to the panels had to be pushed back gently, if levered away during emplacement. It was suggested that the increasing emergence of species was in response to recovery from this disturbance.

Both burrowers had effects on the presence of the visible infauna. Again the effects were different. On addition C. macandreae caused a minor decrease in the surface presence of both Corbula gibba and Amphiura spp. Abundance of both increased again when C. macandreae was confined to its sub-surface galleries. The distribution of Amphiura spp. was unaffected by the activity of C. macandreae. However, the redistribution of C. gibba highlighted two effects previously described for A. chiajei in the defaunated tanks. A number of individuals were redistributed around the two major C. macandreae spoil heaps. The entrances to the burrow system were not vertical like most shafts, but at an angle to the vertical. If the animals were ventilating in their burrow systems, a small localized current could be produced flowing over the spoil heap. As a sedentary suspension feeder (Yonge, 1946a), C. gibba may utilise this current. The other similar effect was that C. gibba moved away from a well burrowed corner (top right hand side of Plate 4.1) where there may have been a high level of sub-surface activity, indicated by the vicinity of four shafts.

Turritella communis showed a definite redistribution around the main C. macandreae spoil heap. Presence in this area would be beneficial as, like C. gibba, it is a ciliary suspension feeder. It feeds close down to the sediment surface (Yonge, 1946b), where it may be able to inhale bottom material from the organic rich heap or make use of the C. macandreae ventilatory current.

Numbers of T. communis remained constant throughout the experimental period.

A major effect was exhibited on the surface visible fauna by the activity of N. norvegicus. In the control area where the crustacean was present for a short period, all the dominant visible fauna except T. communis were affected until the crustacean was removed. In the treatment area there was no recovery even when the N. norvegicus had burrowed down. Emigration of some species may have been responsible for some faunal decrease. However, most of the decrease was probably due to withdrawal into the sediment, burial and mortality. Large amounts of sediment were moved to the sides of the area where the majority of species were relocated. C. gibba if uncoverd was slow to rebury taking up to 30 minutes. This agrees with observations by Yonge (1946a). Stanley (1970) reported that the related species C. caribaea was a very sluggish burrower taking several days to bury if uncovered. Both these authors reported byssal attachment; Yonge (1946a) noted attachment of a thread to a piece of gravel or shell in the sediment. He also suggested that because of its rounded shell and tapering foot, movement would be slow and cumbersome. Maurer et al. (1986) reported that small bivalves that possess a reduced or byssal attachment have virtually no burrowing ability. They also noted that shallow burrowing siphonate suspension feeders should be able to escape a deep overburden of native sediment if buried. C. gibba seems to fit in between these two categories. As a suspension feeder it would not be favoured by the turbid conditions that N. norvegicus can produce. Murphy (1985) has previously reported a reduction in the filtration rate of Mercenaria mercenaria due to an increase in suspended matter from the bioturbatory activities of Callianassa californiensis. Yonge (1946a) did observe, however, that the tip of the foot of C. gibba was on one occasion turned and pushed out through the inhalent siphon, suggesting that this may be a novel method of ejecting sediment from the mantle cavity. Some of these observations also

apply to T. communis as previously discussed in Section 4.4.1. Both these species seem to be poorly adapted to life in unstable areas.

In soft sediments, T. communis is generally replaced by the related species, Aporrhais pespelecani. This latter species has a wide flattened lip to its shell, which may well help support its body weight in soft easily fluidized sediments. It also has specialized feeding and irrigation techniques for a soft sedimentary environment (Yonge, 1937).

Amphiura spp. did not appear to be as affected. When the N. norvegicus was withdrawn into its burrow, their arms were visible at the sediment surface in the shallowest part of the scrape as well as the mounded sediment. Their greater burrowing ability and natural life position is thought responsible for this. However, they were still excluded from the close vicinity of the burrow openings.

4.4.4 Burrower/Burrower Interactions

A number of times N. norevegicus was introduced into an area containing the burrow of C. macandreae and vice versa. In each case the latter was killed. C. macandreae has been reported amongst the stomach contents of N. norvegicus (Oakley, 1979) and may be an important prey species. In the field, however, these two burrowers do coexist, often in high densities (Chapman, 1979). In each case in the laboratory, one was introduced to the burrow of the other. This was artificial in the case of introducing C. macandreae to a N. norvegicus system as they do not normally venture from their own burrows (Nash et al., 1984; this study). Placed in the confines of an aquarium, a burrower would explore the surface and move down any opening present. The occupant, alerted, would investigate. Because of its long chelae, N. norvegicus could easily grab, hold and dismember C. macandreae, consuming some of it and burying the rest.

In the mesocosm, both burrowers produced typical burrows for their species as described in Chapter 2. However, those of C. macandreae did not reach the same complexity nor depth horizon as those in the field and hence N. norvegicus had much easier access to them.

4.4.5 Conclusions

The mesocosm is a useful tool for investigating the pathways of species interactions observed in the field. However, some drawbacks need stressing, notably the impossibility of exactly mimicking natural conditions. Such techniques are perhaps best used in conjunction with field experiments.

The changes in community structure as elicited by the two burrowers have been demonstrated to be quite different, and has resulted in two differing end communities. The activity of both burrowers had both inhibitory and enhancing components, the magnitude of which were dependent on the activity and life mode of the burrower. N. norvegicus, the larger, more surface active burrower, had a greater inhibitive effect, which caused mortality, emigration and a decrease in macrofaunal activity. Direct interaction with the fauna accounted for some of this, but indirect interactions also occurred. Increased turbidity and burial, for example, excluded suspension feeders. A more indirect effect was the inhibition of macrofaunal bioturbation, restricting the living space of associated infaunal species. On the positive side, lack of competition and continual perturbation allowed colonization and maintenance of a small opportunist population.

Burrowing action by C. macandreae had a less marked detrimental effect. Some species disappeared, it was thought by direct interaction. Others, however, were attracted: in particular, the very suspension feeders that were excluded by the N. norvegicus. These were attracted to the organic rich spoil heap, a resource provided indirectly by the C. macandreae.

In the field where the two burrowers coexist, the community as a whole may be constant. On a smaller scale, however, the area would consist of a mosaic of patches of communities determined by resources, refuges and exclusions.

CHAPTER 5. THE EFFECTS OF ORGANIC ENRICHMENT ON MEGAFAUNAL ABUNDANCE

5.1 INTRODUCTION

It has been suggested in this study that megafaunal burrowing species are excluded by high levels of organic enrichment. Pearson & Rosenberg (1976) placed these animals in the 'normal' community at the low input end in their schematic illustration of the faunal and sedimentary changes along an organic enrichment gradient. In a subsequent review Pearson & Rosenberg (1978) noted that as the amount of organic material which reached the sediment increases, larger species and deeper burrowing forms were gradually eliminated to be replaced by different faunal groups. The mechanisms of this process are poorly understood, but the predominant cause is probably the reduction in dissolved oxygen caused by the high biological oxygen demand (BOD) of degradative microbial processes. Bagge & Munch-Petersen (1979) reported that catches of the megafaunal burrower Nephrops norvegicus were negatively correlated to the oxygen saturation of near bottom waters. Catches in the Kattegat were greatest in the month of September when oxygen saturation dropped to 42%. They suggested that even lower levels of oxygen within their burrows forced N. norvegicus out onto the sediment surface. This was further evidenced by the presence of a greater proportion of females in the catches, which are normally confined to their burrows.

The elimination of megafaunal burrowers will have a severe implication for the macrofaunal community, in addition to any direct effect from elevated organic levels. As major bioturbatory processes are removed, large scale transport processes, in particular sedimentary aeration, are inhibited. Conversely, megafaunal disturbance (as outlined in Section 4.4.3) on the macrofauna would also be removed.

In this study megafaunal burrower abundance was investigated along a gradient of organic enrichment at the Garroch Head sludge dumping ground (see following section for full description). The choice of the sludge dumping site gave the chance to investigate a known and well studied organic enrichment gradient, from outwith the dumping ground in towards the centre. The effects of sludge dumping are not, however, confined to direct organic enrichment. Other problems may include the physical effects of sewage sludge, toxicity and the indirect effects on, for example, prey species.

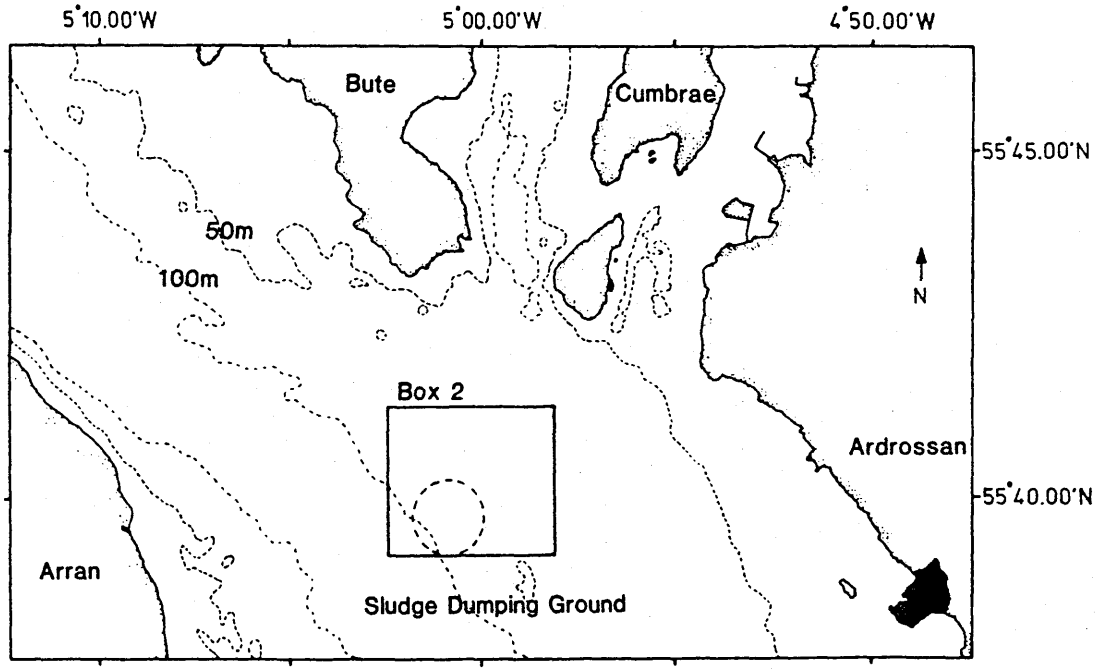
In order to ascertain the point of elimination of megafaunal burrowers and corresponding changes in the macrofaunal community structure and physical characteristics, sampling sites were chosen to correspond with those previously investigated at the macrofaunal level.

Depth of water was such that SCUBA diving was impossible, so sampling was carried out using a towed underwater video sledge. This allowed large areas to be sampled with relatively quick processing of the 'samples'. The use of television underwater dates from the late 1940s and has been reviewed by Barnes (1963) and more recently by Holme (1984). Position fixing using the towing vessel's Decca plotting system allowed the track of the videos to be recorded so that conditions on the sea-bed could be related to previously sampled macrofaunal sites.

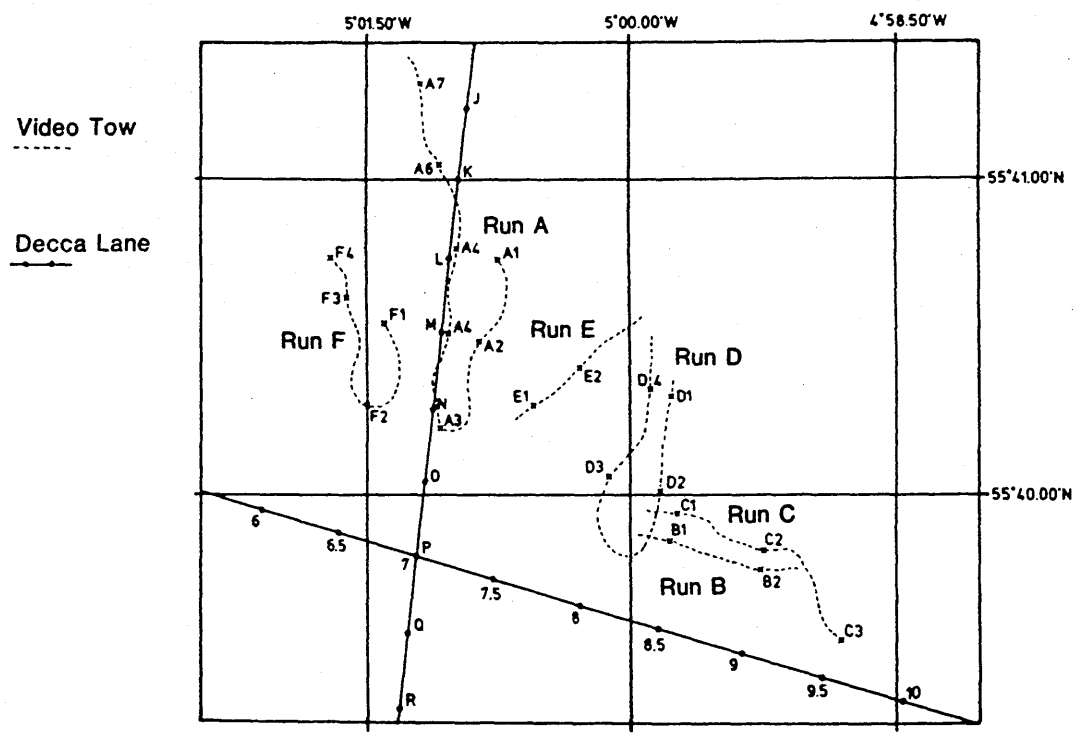
5.2 THE GARROCH HEAD SLUDGE DUMPING SITE

The Garroch Head sludge dumping site is situated approximately 7 km south of Garroch Head, the southernmost point on the Island of Bute in the Firth of Clyde (see Figure 5.1, Box 1). The environment of the site has been monitored annually for a number of years and a series of reports have been produced as to the 'health' of the site (for example Pearson & Blackstock, 1987). The annual survey area has been divided into a box-grid, utilizing existing Decca navigator grid lines; letters denote the approximately east-

Figure 5.1 Box 1 Position of the Garroch Head sludge dumping ground in the Firth of Clyde.



Box 2 Tracks of the video tows in relation to the centre of the dumping ground (P7).



west grid lines and numbers denote the approximately north-south grid lines. Sample sites were situated at a number of intersections of these lines. Those sample sites situated in the area investigated in the course of this present study are indicated in Figure 5.1, Box 2, on the P-line and 7-line (sample sites P6-P10 and J7-R7 respectively). The two transect lines intersect at P7, the approximate centre of the dumping ground.

This site has been well documented by Pearson (1986, 1987). Sewage sludge has been dumped there for many years and is currently dumped at a rate of 1.55×10^6 metric tons per annum. Owing to the general hydrodynamic characteristics of the area, it has been described as an accumulating sludge disposal site, with a general depth of water of 70-80 m, but in excess of 100 m on the south-west side of the area. The bottom sediments are predominately fine silt clays, with a background carbon content of 2-3%. This is elevated in the centre of the ground to 7-12% as most of the sedimentary material settles rapidly out of the water column within the 6 km^2 designated area. Pearson (1986) noted further that the high carbon content coincided with reduced sedimentary conditions (negative Eh) and elevated values of a range of metal elements and other anthropogenic material. Some small patches of sandier sediments do occur to the north-east of the dump centre as dredged material from an oil-rig fabrication yard were previously dumped there.

5.3 METHODS AND MATERIALS

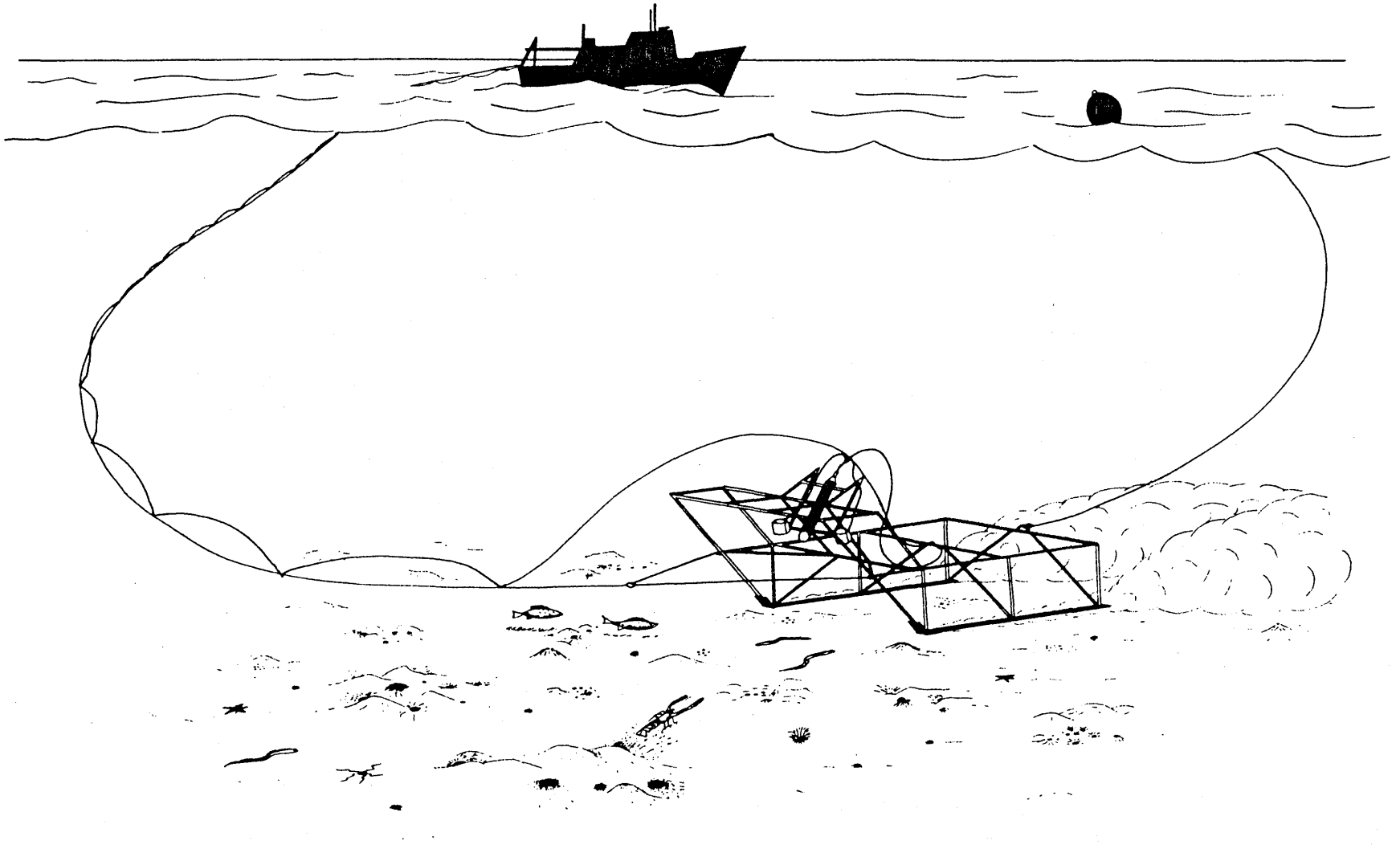
Observations were made during two cruises on R.V. Aora (3-4.6.87) The video sledge was deployed from the stern of the vessel on a steel warp with the camera control umbilical loosely attached every few metres. A course could be maintained, but due to the necessary slow speed of the sledge across the ground, it was dependent to a certain extent on the prevailing wind. Six tows of variable duration were completed.

The recording apparatus consisted of a monochrome silicon diode array television camera (Hydroproducts TC125 SDA), mounted on the metal framed sledge with the camera orientated to look obliquely downwards. Artificial light was provided by two 250W quartz iodide lamps (Hydroproducts HQ250), fitted with red acrylic filters. These reduced the disturbance effects of the light on N. norvegicus as analysis of the spectral response curve of the visual pigment indicates little responsiveness to red light (Loew, 1976). The resolution of the camera in conjunction with image blurring caused by the moving sledge limited accurate identification of small objects (approximately less than 2 cm diameter). Recording was done aboard the vessel using a VHS video recorder (National NV3051), powered by the vessel's generator. Figure 5.2 illustrates the video sledge as it would be towed along the sea-bed. In the water the sledge had extra weights along the sledge runners and was buoyed along its top and front to provide stability.

Recordings were made for the whole time that the sledge was on the sea-bed. These were later analysed in the laboratory. From each of the plots of the tows (see Figure 5.1, Box 2) sample sites were selected. One hundred square metres of sea-bed were then analysed at the corresponding section of video tape. The abundance of various features/species was then enumerated and investigated. Position fixing of the sample sites along the video tows relied on assuming constant velocity of the surface vessel (particular attention was given to the tow speed during operations, so this assumption is reasonably valid, though some variation occurred). An elapsed time was calculated to reach a certain point on the plot of the tow and the video tape was analysed at that specific time. Positioning was thought to be accurate to approximately plus or minus 200 m.

The Jaccard coefficient based on the presence and absence of species was used to calculate the similarity between the different sample sites.

Figure 5.2 Illustration of the towed video sledge in action on the seabed.



Cluster analysis (using CLUSTAN2, Heriot-Watt University computing), which utilized group average sorting produced a dendrogram of the results.

5.4 RESULTS

5.4.1 Megafaunal Abundance at Garroch Head

The details of each of the tows illustrated in Figure 5.2, Box 2, are shown in Table 5.1. There were six tows, aimed roughly parallel to the north-south '7' line and the east-west 'P' line. Three of the tows, A, D and F, started outside of the dump area in relatively well burrowed areas, towed in towards the centre of the ground and then out again. Tows B, C and E started within the dumping ground and headed out towards well-burrowed areas. Tows were normally terminated when stable bottom conditions were observed over a large area. The burrowed area had a degree of topographical relief whereas the 'polluted' area of the sea-bed adjacent to the centre of the dumping area was very flat, grainy in appearance and often covered in a white mat of thiophylletic bacteria, probably Beggiatoa spp. and larger anthropogenic debris. The Beggiatoa did not extend into the burrowed area but was confined to the central area of the dump site.

The abundance of the various visible features and species for each of the 22 sample stations along the video tows is shown in Table 5.2. Burrow entrances were defined as large holes (diameter greater than approximately 2 cm) in the sediment surface that were most probably attributable to megafaunal action. Nephrops norvegicus and Calocaris macandreae systems were defined as individual discrete burrows encompassing a number of characteristic openings. Individual N. norvegicus were observed at times on the sediment surface or in an opening to their burrows. These individuals were not, however, enumerated as it was felt that they would not make a representative count, as other unobserved individuals may have been present in

Table 5.1 Technical data for the video tows plotted in Figure 5.2.

Tow	Time in	Time out	Duration (mins)	Distance (m)	Speed m/min
A	0921	1107	106	3621	34.16
B	1138	1216	38	1017	26.76
C	1330	1445	75	1587	21.16
D	0900	1055	115	2689	23.38
E	1119	1206	47	996	21.19
F	1334	1415	41	1683	41.05

Table 5.2 Abundance of megafaunal features/species across Garroch Head Sludge Dumping Ground (m^{-2}) at each of the 'sample' sites.

Sample Site	Burrow Entrances	*Nephrops* systems	*Calocaris* systems	*Lumpenus lampretaeformis*	*Callianassa* mounds	*Cepola* systems	Cerianthid anemonies	*Buccinum*	Hermit Crabs
A 1	1.20	0.16	0.01	0.02	-	-	0.34	0.23	-
2	-	-	-	-	-	-	0.01	-	-
3	-	-	-	-	-	-	0.07	-	-
4	0.43	0.09	0.03	0.03	-	-	0.18	0.1	0.03
5	1.76	0.27	0.12	0.11	0.1	-	0.12	0.01	0.04
6	4.86	0.8	0.48	0.07	-	-	0.03	0.05	0.01
7	3.44	0.27	0.64	0.05	-	-	0.07	0.07	0.13
B 1	-	-	-	-	-	-	0.12	-	-
2	5.21	0.5	0.78	0.17	-	-	-	0.03	0.03
C 1	0.08	0.02	-	-	-	-	0.16	0.1	0.02
2	4.49	0.45	0.51	0.13	0.01	-	0.12	0.05	0.14
3	7.04	0.61	1.12	0.12	-	-	0.17	0.08	0.08
D 1	3.52	0.45	0.54	0.17	0.04	-	-	0.01	-
2	0.01	0.02	-	0.04	-	-	1.16	0.11	0.08
3	0.07	0.02	-	0.03	-	-	0.20	0.04	-
4	4.41	0.63	0.89	0.13	0.02	0.04	0.03	0.04	0.02
E 1	0.05	0.04	-	0.01	-	-	1.04	0.06	0.02
2	4.88	0.40	0.65	0.12	-	-	-	0.06	0.02
F 1	-	-	-	0.01	-	-	0.2	0.02	-
2	-	-	-	-	-	-	0.02	-	-
3	0.05	0.01	-	-	-	-	0.56	0.02	0.02
4	1.37	0.26	0.17	0.04	-	-	0.03	0.09	0.02

their burrows. Callianassid mounds were defined as the number of mounds observed that were a typical surface feature of the burrow of Callianassa subterranea (or in light of the evidence from Chapter 2, Jaxea nocturna or Maxmulleria lankesteri). Individuals of the burrowing snake blenny Lumpenus lampretaeformis were counted when on the sediment surface, owing to their small burrow entrances and the inability to identify these from the videos. they were often observed in pairs, swimming in front of the video sledge. The distribution of these fish suggested that they may have been territorial. Four burrows belonging to the red-band fish, Cepola rubescens, were observed in one clump at site D4. These burrows were as described by Atkinson et al. (1977) and Atkinson & Nash (1985). Identification was aided by the presence of an individual that swam out of its burrow and out of screen view. All the aforementioned species were noted as megafaunal burrowers.

The anemones observed were large burrowing cerianthids (Cerianthus lloydii - oral disc diameter greater than approximately 2 cm). Smaller individuals may well have been present, but were not observed due to the limited definition of the video camera. Buccinum undatum and hermit crabs (mostly Pagurus bernhardus), both mobile epifaunal scavengers, were persistently present at most of the sample sites and were recorded to see if their abundances were also affected by organic enrichment.

A number of fish species were observed along the video hauls but were not included within the data in Table 5.2, these included, Pollachius virens (saithe), Clupea harengus (herring) and several unidentified flatfish. It was thought that these species were transitory by nature and would not represent or characterize any one particular area.

To investigate the change in abundance of these features/species as the centre of the dump ground was approached, the sample stations were re-ordered. The centre of the dump is not centred exactly on P7, but extends slightly up the 7-line and for some distance away from both sides

of P7 on the P-line. The sample stations were therefore ranked according to their distance from a line drawn roughly between O7 and P9. Thus A7 was the furthest site from, the centre of the dump and A3 the nearest site. The abundance data were converted to a log (100x+1) format to bring all the features/species to the same scale for more accurate comparative purposes. This was then plotted in Fig. 5.3. From left to front right the axis is one of decreasing distance to the centre of the dumping area, which was defined as a gradient of increasing organic enrichment. The vertical axis is the log-transformed abundance. Each feature/species was overlayed on the following feature/species.

Generally, the abundance of megafaunal burrowing species decreased with increasing organic enrichment. This was not, however, smooth and there was some variation; in particular, lower abundances were observed at sites A1 and A5 compared to other sites within a comparable distance of the dump centre. The snake blenny L. lampretaeformis extended furthest into the dump centre. The burrows of N. norvegicus followed the abundance of total megafaunal burrow entrances and were a fairly constant proportion of this. C. macandreae did not extend as far along the enrichment gradient and exhibited a greater degree of variation in abundance than the previous species. The abundance of B. undatum and hermit crabs was low and variable and neither extended into areas of high enrichment. Cerianthid anemones did, however, extend to the sample site nearest the centre of the dump grounds. Again their abundance was highly variable. Their maximum occurrence was at an intermediate high level of enrichment, but they were less abundant at sites where the larger burrowers were more abundant.

The spatial distributions of the dominant megafaunal burrowers were mapped in Figures 5.4-5.7. The total abundance of megafaunal burrow openings and the abundance of N. norvegicus burrow systems, showed an identical distribution for the given contours. There were a number of well

Figure 5.3 Change in relative abundance of megafaunal species/features with increasing organic enrichment. Stations are ordered in terms of decreasing distance from the dump centre, which is: A7, A6, C3, A5, A1, D4, D1, B2, C2, E2, F4, A4, D2, C1, F3, B1, D3, E1, A2, F1, F2, A3.

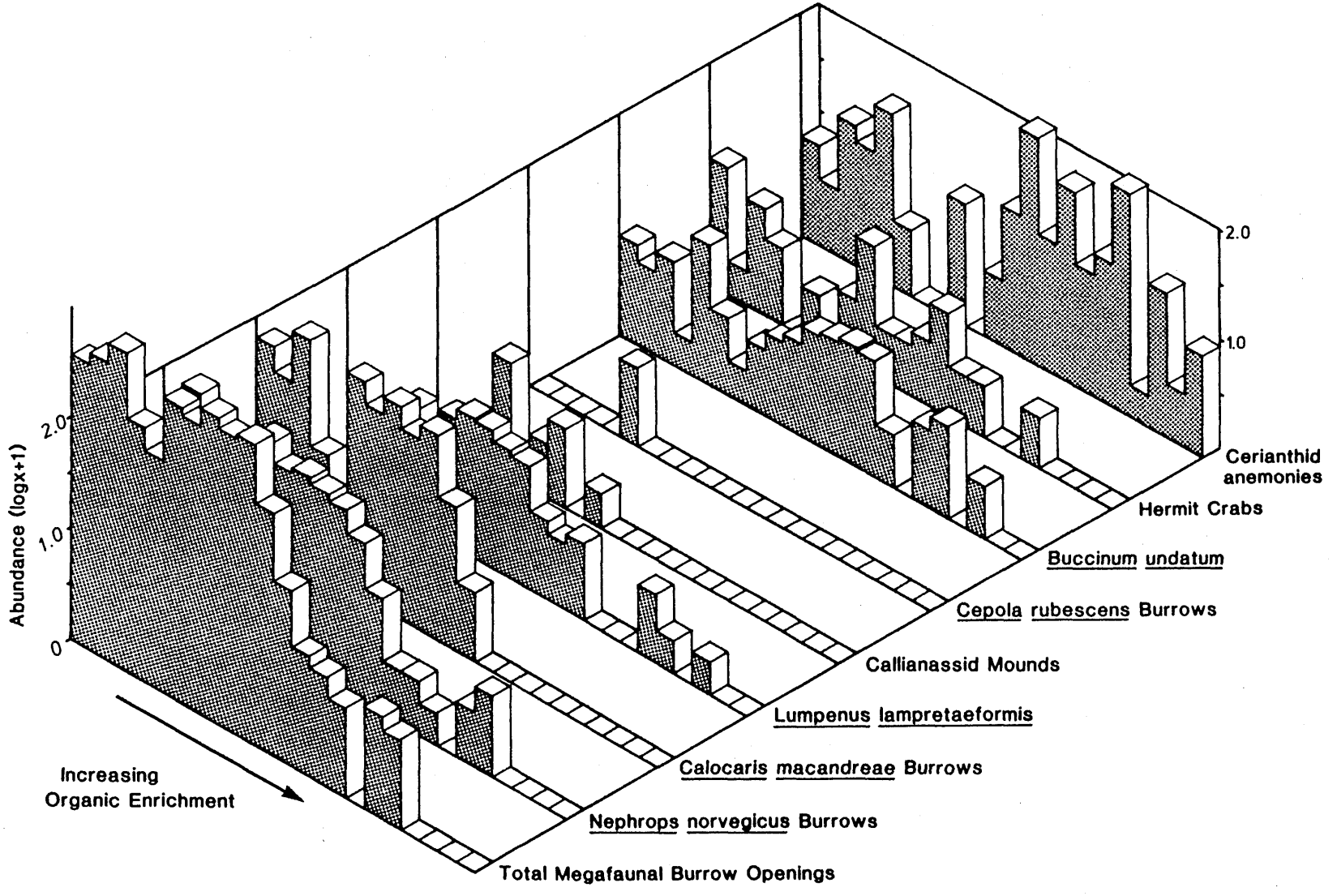


Figure 5.4 Distribution of megafaunal burrow openings to the north of the Garroch Head sludge dumping ground

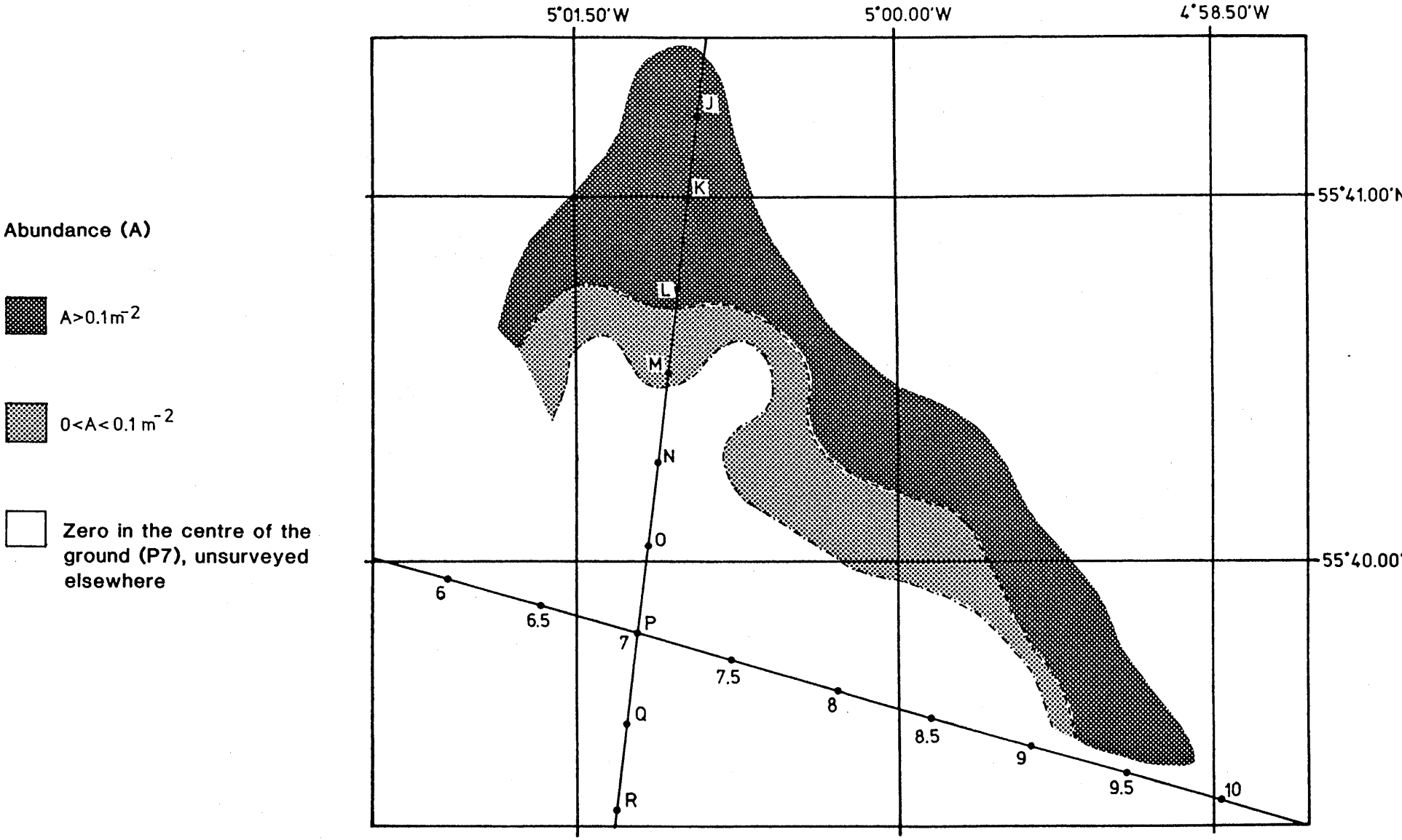


Figure 5.5 Distribution of Nephrops norvegicus burrows to the north of the Garroch Head sludge dumping ground.

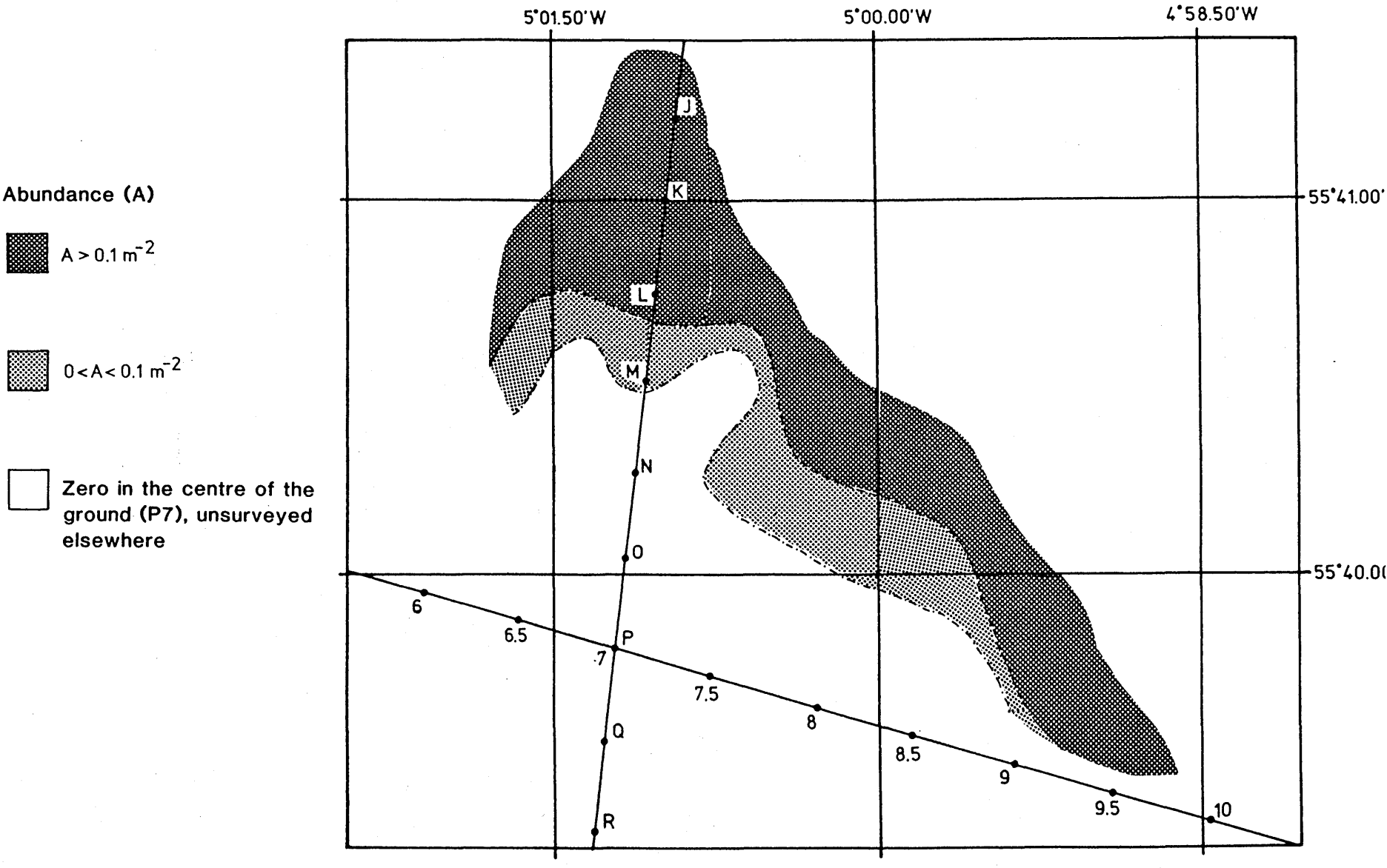


Figure 5.6 Distribution of Calocaris macandreae burrows to the north of the Garroch Head sludge dumping ground.

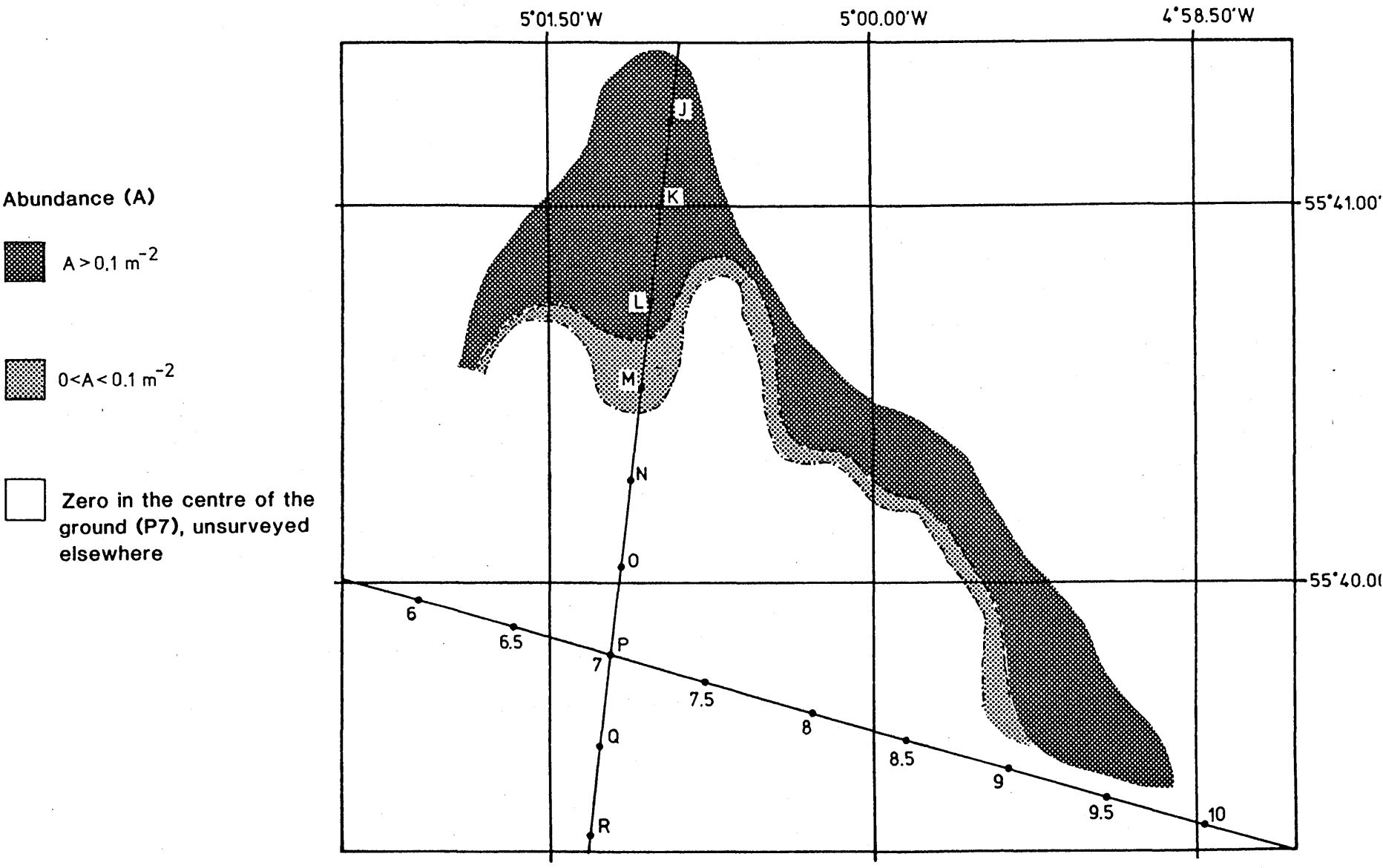
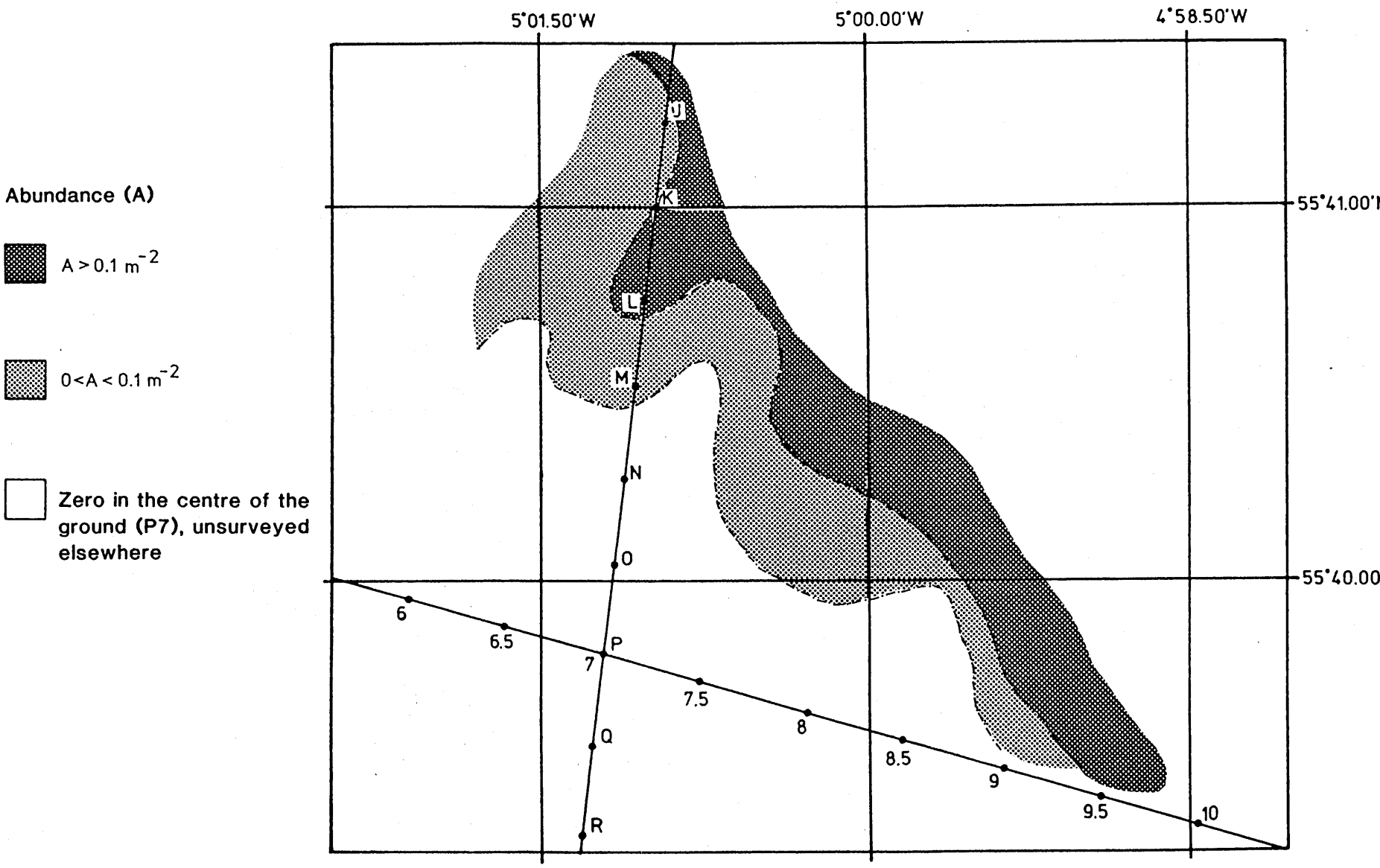


Figure 5.7 Distribution of Lumpenus lampretaeformis individuals to the north of the Garroch Head sludge dumping ground.



burrowed outer sites (abundance < 0.01^{-2}), a transition zone with an intermediate abundance (< 0.1 m^{-2}) and an inner area devoid of burrows. The increase in abundance away from the centre of the dumping ground was not equal at equidistant sites away from P7. Site A4 seemed to be in the transition zone, but was adjacent to two sites without megafauna (F1 and A2). Maximum abundance of N. norvegicus burrows was observed at sample site D4 (0.64 m^{-2}) with other high abundances at sites C2, C3 and D1 (0.45 m^{-2}), 0.61 m^{-2} and 0.45 m^{-2} respectively). Maximum abundance of total megafaunal burrow openings was 7.04 m^{-2} at site C3 with abundances in excess of 4 m^{-2} at sites A6, B2, C2, D4 and E2.

The distribution of C. macandreae burrows in Figure 5.6 did not extend as far into the dumping area as the two previous features. Again significant abundance at site A4 trespassed into the area of nil abundance. Maximum abundance of these burrow systems was 1.12 m^{-2} at sample site C3 at the eastern end of the dumping ground.

Abundance of L. lampretaeformis was relatively low compared to that of the other megafaunal burrowers, not exceeding 0.17 m^{-2} (sample sites B2 and D1). This species extended some way into the dumping ground, but its distribution west of the 7-line was very limited (Figure 5.7). In agreement with the other megafaunal burrowers, there was a higher abundance at A4 than at the two adjacent sites, A2 and F2.

The abundance of cerianthid anemones was too variable between sites to contour smoothly. Maximum abundance was 1.16 m^{-2} at site D2 and 1.04 m^{-2} at site E1.

5.4.2 Sample Site Similarities at Garroch Head

Based on the data in Table 5.2, percentage similarities were calculated between all the sites using Jaccard's Coefficient (based on the presence and absence of features/species). The sites were ordered in terms of increasing

distance away from the centre of the dumping ground and decreasing organic enrichment. The data matrix is shown in Figure 5.8. Two major and a number of minor clusters were evident of high percentage similarity. The two major clusters included one from the 'polluted' centre area of the dumping ground (sites A2, A3, B1, F2) and one from the outer, cleaner area of the ground, including most of the northerly and easterly sites (sites A4, A6, A7, C3, F4). The small clusters of high similarity were mostly in the transitionary zone as portrayed in Figure 5.4 (sites D2 and E1, C1 and F3, B2 and E2, A5 and C2). Using cluster analysis, a somewhat different ordering of stations was reached. This is illustrated by the dendrogram in Figure 5.9. The sequential chaining is indicative of an environmental gradient. This figure shows the clusters more clearly with a distinct difference between the 'polluted' centre sites (A2, A3, B1, F2) and the other less polluted sites. The difference in ordering along the axis, compared to that based on distance from the centre of the site, is indicative perhaps of irregular dumping.

5.5 DISCUSSION

5.5.1 The Use of Video in Megafaunal Surveys

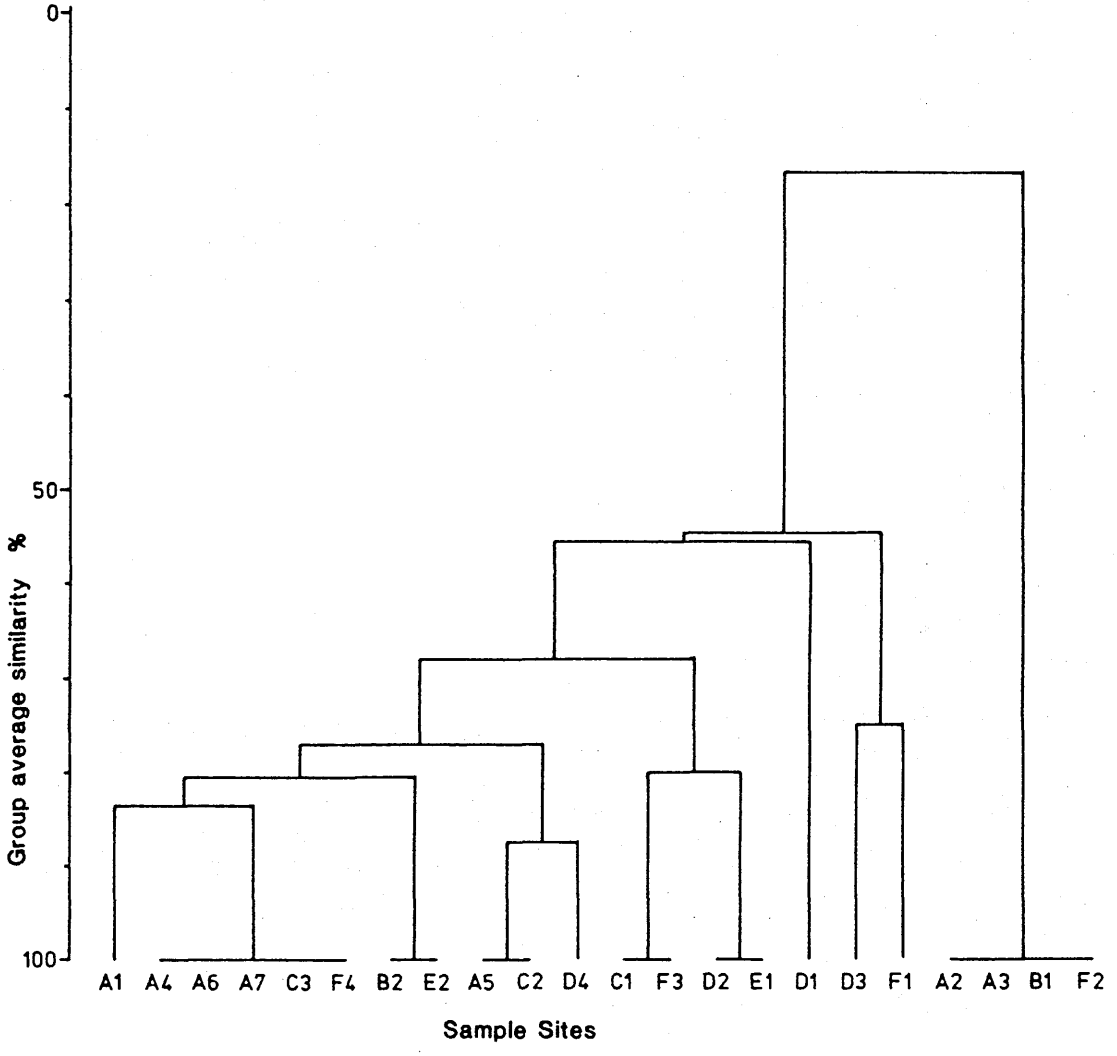
The use of underwater video for this survey allowed a large area of sea-bed to be surveyed in a relatively short period of time. It was possible to quantify the density of large animals of low abundance, in a way not possible with any accuracy by other methods (grabs, dredges or trawls). Video cameras are often used in conjunction with other gear during extensive surveys, for a visual appraisal of bottom conditions, but incidences of published data from the use of this method are relatively low. Holme (1984) has, however, recently reviewed the literature on the use of underwater photography and television. Previous use of underwater television in the

Figure 5.8 Percentage similarity matrix of the 'sample' sites at the Garroch Head sludge dumping ground, based on megafaunal species/features using Jaccards coefficient.

	A3	F2	F1	A2	E1	D3	B1	F3	C1	D2	A4	F4	E2	C2	B2	D1	D4	A1	A5	C3	A6	A7
A3																						
F2	100																					
F1	33	33																				
A2	100	100	33																			
E1	20	20	60	20																		
D3	25	25	75	25	80																	
B1	100	100	33	100	20	25																
F3	25	25	40	25	80	60	25															
C1	25	25	40	25	80	60	25	100														
D2	20	20	33	20	100	80	20	80	80													
A4	17	17	50	17	83	67	17	67	67	83												
F4	17	17	50	17	83	67	17	67	67	83	100											
E2	0	0	33	0	67	50	0	50	50	67	83	83										
C2	14	14	43	14	72	57	14	57	57	72	86	86	72									
B2	0	0	33	0	67	50	0	50	50	67	83	83	100	72								
D1	0	0	33	0	43	50	0	43	43	43	57	57	67	72	67							
D4	13	13	38	13	63	50	13	50	50	63	75	75	63	88	63	63						
A1	20	20	60	20	67	80	20	50	50	67	83	83	67	71	67	67	63					
A5	14	14	43	14	72	57	14	57	57	72	86	86	72	100	72	72	88	72				
C3	17	17	50	17	83	67	17	67	67	83	100	100	83	86	83	57	75	83	86			
A6	17	17	50	17	83	67	17	67	67	83	100	100	83	86	83	57	75	83	86	100		
A7	17	17	50	17	83	67	17	67	67	83	100	100	83	86	83	57	75	83	86	100	100	

0 - 49% 50 - 74% 75 - 99% 100%

Figure 5.9 Dendrogram illustrating the similarity between the megafaunal 'sample' sites at the Garroch Head sludge dumping ground based on Jaccards coefficient of similarity and group average sorting.



estimation of the abundance of Nephrops norvegicus has been reported in Bailey et al. (1986).

The accuracy and use of this technique has its limitations. One previous sampling trip was aborted due to continual rough weather. This did not restrict the deployment of the gear, but increased the turbidity in the water column. Visibility was, therefore, reduced to less than a metre and the television lights caused further problems with backscatter of light from larger particulate matter. The camera tube used suffered somewhat from 'burn-in' (long term retention of brightly lit scene) and 'lag' (short-term image retention), which caused an overall blurring and comet tailing of moving image (Holme, 1984). In the latter case, the moving image was effectively the sea-bed. The resolution was, therefore, limited to larger objects and prevented the identification of smaller features. Other limitations of the particular gear used included depth limitation to less than 85 m due to umbilical length and accuracy of the distance covered from reliance on a copy of the ship's plotter.

Chapman (1979) noted that estimates of burrow densities were likely to overestimate the number of N. norvegicus present because of the presence of uninhabited burrows and a variable number of openings per burrow. However, only burrow densities were given in this study as they are the visible evidence of sediment disturbance. These densities could be converted to the approximate individual abundances by using the value for 30% occupancy estimated in Chapter 2.

It is felt that, despite the limitations, underwater video is a very useful tool for estimating the abundance of large epibenthic features and is perhaps at its most useful combined with other methods of survey for more detailed benthic analysis.

5.5.2 Synopsis of the Garroch Head Survey

5.5.2.1 The Effects of Sludge on the Physical Environment

The effects of sludge dumping at Garroch Head on some of the physical parameters of the sediments is shown in Table 5.3 (from Pearson & Blackstock, 1987). As can be seen the sedimentary organic carbon and nitrogen increased towards the centre of the dumping ground, carbon from approximately 3% to over 10% at P7. This seems relatively low compared to the actual 20 gm^{-2} of dry sludge that is dumped per day over the centre area of the site (Pearson, 1987) which was noted as one to two orders of magnitude higher than the highest levels of natural input to inshore sediments. However, the value given for P7 may reflect a high rate of degradative processes (both microbial and macrofaunal) that can accommodate the carbon input. The lower carbon:nitrogen ratio at P7 may be indicative of this high microbial activity.

The redox potential at 40 mm depth decreased in value towards the dump centre. Pearson & Stanley (1979) and Rhoads & Boyer (1982) observed that negative redox potentials were linked to organic loading and that they indicated highly reduced conditions associated with the high biological and chemical oxygen demands of degradative processes. Reducing conditions were confined to an area encompassed by the stations P6-P8.5 and northwards to, but not including, station N7. Reducing conditions are indicative of a lack of bioturbation and vice versa, as bioturbation is a major chemical transport mechanism, normally responsible for sediment oxygenation (Rhoads, 1974). Lack of megafaunal bioturbation was evidenced by their absence from this area. Runs A and D came closest into the centre of the ground, but did not approach any closer as it was obvious that the areas covered were already well into the dump centre and that megafaunal burrowers were absent.

Table 5.3 Physical and biological data at various sites from the Garroch Head Survey (from Pearson & Blackstock, 1987). Includes organic carbon content (%C), nitrogen content (%N), carbon to nitrogen ratio (C:N), redox potential at 40 mm sediment depth (Eh), species number (S), abundance (A), biomass (B), abundance ratio (A/S) and size ratio (B/A).

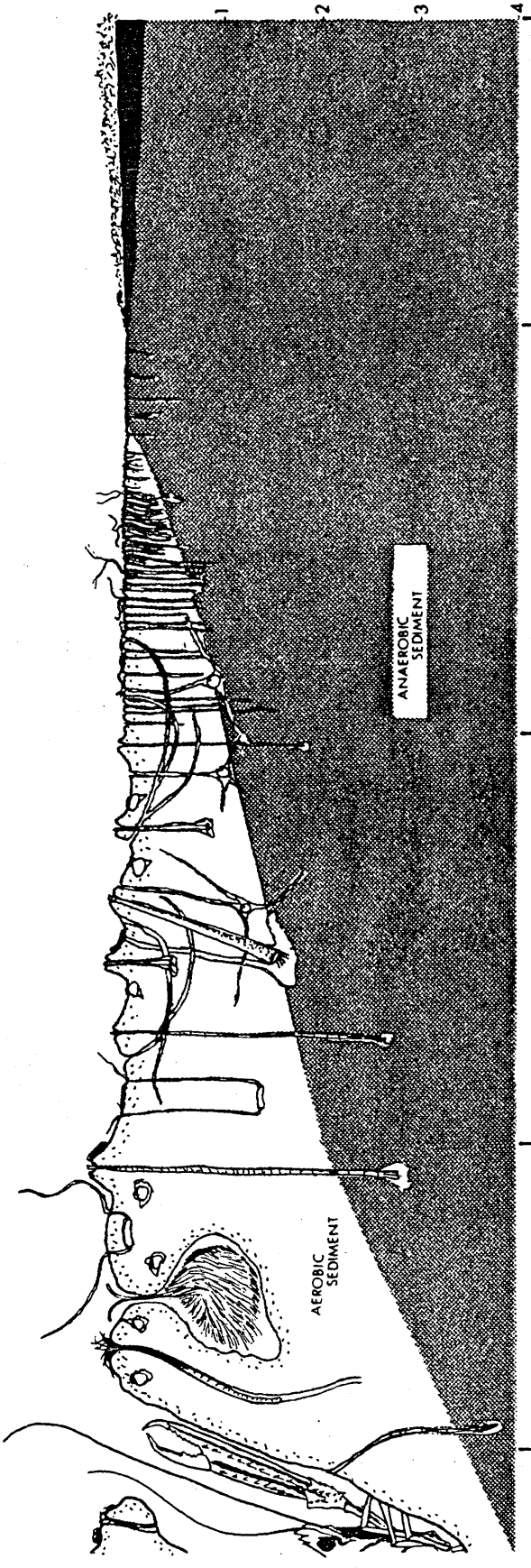
Sample Site	%C	%N	C:N	Eh (mV)	H	e	S	A	B	A/S B/A
J 7	3.0	0.15	19.8	+ 071	3.25	0.55	46	305	247	6.5 85.8×10^{-3}
K 7	3.5	0.17	20.5	+ 100						
L 7	3.9	0.25	15.5	+ 041						
M 7	6.0	0.53	11.3	+ 007	1.27	0.11	25	5844	526	234.7 9.25×10^{-3}
N 7	9.0	0.70	12.8	+ 029						
P7	10.4	0.83	12.5	- 144	0.75	0.27	5	2797	155	559.4 5.45×10^{-3}
P6	5.7	0.48	11.8	- 063						
P 8	4.6	0.38	12.2	- 159						
P 8.5	3.5	0.29	12.1	- 094	1.43	0.18	24	3722	252	274.5 6.35×10^{-3}
P 9	1.5	0.12	12.6	+ 109						
P 9.5	2.9	0.22	13.1	+ 024						
P 10	3.1	0.27	11.5	+ 120	3.03	0.60	34	210	129	6.4 138.9×10^{-3}

In terms of the carbon content of the sediments, on the 7-line, the megafaunal burrowing community was absent from areas of greater than 6% organic carbon but were abundant in areas of less than 4%. Correlating the abundance of the P-line was more difficult as 'sample' sites were not so close. A gradient of increasing organic content was not so evident at this side of the dumping ground, which may well reflect a more spasmodic occurrence of dumping in this area. The burrowing community was abundant at site C3 adjacent to P9.5 with an organic content of 2.9%, similar to that at J7 on the 7-line.

5.5.2.2 The Effects of Sludge on the Benthic Community Structure

The macrofaunal community data from the Garroch Head survey for the area covered in this study is shown with the physical data in Table 5.3 (from Pearson & Blackstock, 1987). Owing to a specified sampling strategy, macrofaunal analysis was limited to a small number of representative stations, which included sites J7, M7, P7, P8.5 and P10. Thus data were presented for two gradients, entering the dump centre from the north and east of the ground. Clear gradients have been demonstrated with the physical data and were also evident from the biological data with: decrease in diversity (H'), decrease then slight increase in evenness (e), decrease in the number of species (S), large increase then slight decrease in abundance (A), increase then decrease in biomass (B), increase in abundance ratio (A/S - carrying capacity) and decrease in size ratio (B/A - community structure).

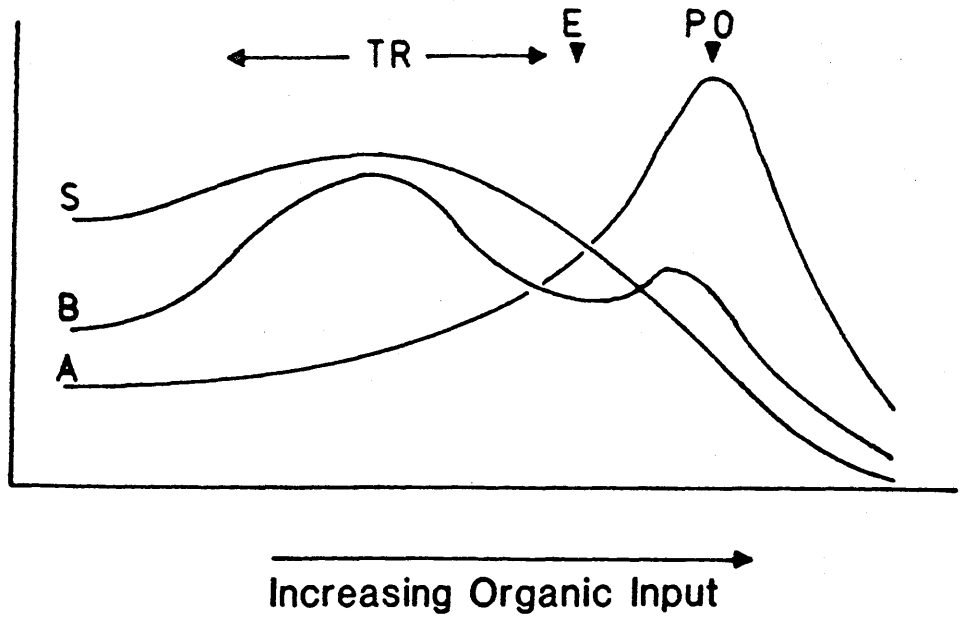
The changes in biological data as the dump centre was approached were all characteristic of the changes in community structure ascribed by Pearson & Rosenberg (1978) to a gradient of organic enrichment. A schematic illustration was presented by Pearson & Rosenberg (1976) and is shown in Figure 5.10, whilst the generalized change in community statistics for this type of gradient is shown in Figure 5.11. The two sites J7 and P10 could be said to be relative normal on the scale of change. This corresponded to the



ZONE	NORMAL	TRANSITORY		POLLUTED	GROSSLY POLLUTED
TYPICAL MACRO FAUNA DOMI-NANTS	Nucula Amphiura Terebellides Rhodine Echinocardium Nephrops	Labidoplax Corbula Goniada Thyasira Pholoe	Chaetozone Anaitides Pectinaria Myriochele Ophiodromus	Capitella Scolelepis	No MACROFAUNA Surface covered by fiber 'blanket'

Figure 5.10 Diagram of changes in fauna and sediment structure along a gradient of organic enrichment (from Pearson & Rosenberg, 1976).

Figure 5.11 Generalized change in species number (S), abundance (A) and biomass (B) along a gradient of organic enrichment: PO, peak of opportunists: E, ecotone point: TR, transition zone (from Pearson & Rosenberg, 1978).



well burrowed area, inhabited by a wide range of megafaunal species. The sites M7 and P8.5 corresponded to the peak of opportunists in Figure 5.11 or polluted zone in Figure 5.10. On the northern side of the dumping ground, this corresponded to the area of very low megafaunal abundance, whilst on the eastern side of the ground there were none present. The megafaunal data from the M7 area may be slightly anomalous for two reasons. Firstly, there may have been a position fixing error, as discussed in Section 5.3. Secondly, the burrows in this area were not abundant and may have been relict structure from cleaner times. Burrows have remained intact for over a year in the aquarium after the occupant had died (personal observations). Field observations have, however, suggested that burrows may only last 2-3 weeks (pers. comm., R.J.A. Atkinson). The P7 site corresponded to the more polluted side of the opportunists' peak in Figure 5.11.

The megafaunal transition zone appeared to correspond with sites L7 and P9.5. On the idealized gradient, this would also be expected to be the area of macrofaunal transition. However, no recent macrofaunal data are available for these sites. Only the gross changes can be observed between the clean and polluted areas, with respect to the macrofauna. There is a change from a mixed community to predominately surface deposit feeders (Pearson & Blackstock, 1987). This may in some part be due to the absence of megafaunal burrowing species and associated bioturbation, which is discussed in Section 5.5.4.1.

5.5.3 The Distribution of Megafaunal Species at Garroch Head

The Garroch Head sewage dumping ground was undoubtedly a Nephrops norvegicus ground prior to the advent of dumping (McIntyre & Johnston, 1975). General observations from this study agreed with an earlier television study of the area reported in McIntyre & Johnston (1975), which showed a clear transition from N. norvegicus ground to black mud of fibrous texture which

would inhibit normal burrowing. An estimated 10 km^2 of former ground had been made unsuitable for this species. No such estimates for this study could be made as only one quadrant of the dumping ground was investigated.

The burrows of C. macandreae were recorded in abundance in the N. norvegicus burrowed area, having a similar distribution. This crustacean is commonly found in areas burrowed by N. norvegicus (Chapman, 1979, 1980). However, it may have been more affected by the sewage sludge as it did not appear to extend quite so far into the dump area.

Callianassa subterranea (a category which probably includes other mound-builders) was only observed at four of the sample sites in the outer dump area. Abundance was very low which may have been related more to such factors as sediment type rather than the effects of sludge deposition.

The burrowing snake blenny Lumpenus lampretaeformis was not very abundant. However, it was present in areas lacking other megafaunal burrowers. Its distribution was somewhat limited to the shallower eastern side of the dump area. Wheeler (1979) noted that it was most abundant at 40-100 m, so it is unlikely to be principally depth regulated. L. lampretaeformis might well appear to have a patchy distribution, but if it is largely territorial as observations suggested, it may have a low and constant abundance throughout the area which the scale of sampling could not detect. High densities of L. lampretaeformis have been maintained in the aquaria by Atkinson et al. (1987) with no reported territorial behaviour nor pairing. They reported the presence of interconnecting burrows, but their significance was unknown.

The other burrowing fish, Cepola rubescens, was not widely distributed and was only identified at one site, in the well burrowed outer region of the dumping ground. It has been commonly collected closer into the Ayrshire coast (Atkinson et al., 1987), south of Ardrossan (see Figure 5.1). Its absence from large areas of Garroch Head was probably more a function of sediment

type. The observation of all the burrows in one clump agreed with reports by Atkinson et al. (1977). They suggested that biological and/or physical factors were involved in determining this aggregation, such as reproductive behaviour or substratum differences. (It may be significant that sandy sediments were dumped in this region following coastal dredging.)

Of the large non-actively burrowing species, the whelk Buccinum undatum and the hermit crab Pagurus bernhardus were observed outwith the dump centre and never in very high abundance. Both are food generalists and largely opportunistic (Taylor, 1978 and Jackson, 1913, respectively). B. undatum has previously been reported to have highest abundance in and around the sludge disposal area (Halcrow et al., 1973).

Cerianthus lloydii had its highest abundance in the more polluted areas of the dumping ground, although from earlier observation it was not abundant in the dump centre. This is a tubiculous species which lives mostly at the sediment surface retracting into its tube for protection. The tube consists of mucous bound sediment and is thick and matted in nature, which may give some measure of protection from such factors as high sulphide levels in anaerobic sediments. The abundance pattern of C. lloydii in the ground may be controlled by a number of factors. It would be favoured by sewage input, a food resource, as cerianthids respond positively to high levels of particulate organic matter (Arai & Walder, 1973; Tiffon, 1976). Eleftheriou & Basford (1983) also showed that C. lloydii fed largely on itinerant benthic, planktonic and hyperbenthic crustaceans, the latter two having been shown to be abundant at the Garroch Head ground (McIntyre & Johnston, 1975). However, in towards the centre, cerianthid abundance may be limited by clogging from higher sludge deposition rates. Lastly, its abundance could be affected by disturbance from megafaunal burrowing activity, as cerianthid abundance was lowest in the areas of high burrow incidence.

5.5.4 The Mechanism of Sludge Effects on the Benthic Ecosystem

Sludge dumping may have a range of effects on the sea-bed and its inhabitants. In the water column the addition of sludge may cause eutrophication and algal blooming through nutrient addition. This may result in anoxia from the decomposition of excess deposits of algae.

Within the sediment, the physical effects of the sludge may cause burial of some bottom dwelling species, excess turbidity or a change in sedimentary characteristics resulting, for example, in their inability to construct and maintain burrows. Sewage sludge from industrial and domestic sources also contains many substances which may be toxic in the amounts dumped or may reach toxic levels by accumulation through the food chain.

The high carbon content of the sludge reaching the sediment may lead to a high biological and chemical oxygen demand and hence anoxia in the sediments and possible hypoxia and intermittent anoxia in the near bottom waters. Anaerobic degradation may also lead to a build up of toxic sulphide within the sediment.

The response of individuals to any of these effects can exist at a number of hierarchical levels. Bayne (1985), characterized two of these: the primary response, mostly at the neuro-hormonal level and the secondary response, the physiological consequences of the primary response, mostly at the respiratory and metabolic level. Further responses which follow at a higher level could include individual behavioural responses (for example increased emergence at the sediment surface or reduced feeding activity), and community responses, as interactions such as competition, predation and recruitment are affected. The first three types of response would not be evenly elicited across a whole community as each individual species would react differently. Even within a species there may be some difference in reaction due to individual variation.

Certain developmental stages of benthic invertebrates may be more susceptible to changes in the environment, in particular juvenile stages.

Changes in sediment type may mask settlement 'triggers', thus preventing settlement and continued maintenance of a particular species. Juvenile stages may also be less tolerant to such factors as low sediment oxygen and high sulphide concentrations.

For predatory megafaunal burrowing species (Lumpenus lampretaeformis and Nephrops norvegicus), effects may be more indirect, through any of the aforementioned factors affecting their prey species.

In the case of the Garroch Head site, Pearson (1986) noted that there was neither significant transference of metals beyond the central contaminated dump area and nor was there a general accumulation in the finfish and shellfish of the area. Although no studies of water column eutrophication have been made, he pointed out that there was no evidence to suggest that bloom conditions had occurred through increased nutrient availability.

The sludge effects that are thought to be important are: the change in sedimentary characteristics, the effects on juvenile forms, the changes in interactive processes and the promotion of anaerobic conditions.

5.5.4.1 Change in Sedimentary Characteristics

There are two aspects to sludge dumping that could cause change in sedimentary characteristics. Firstly, the direct input of fine particulate matter would cause a decrease in median grain size. Secondly, and more indirectly, if certain bioturbators are affected, so would be their activity, which may be of importance in maintaining particular sedimentary characteristics (for example, pore water content or particle bedding - see Chapter 1). Sedimentary modification and unsuitability have been postulated as the reason for low or variable abundance of some of the megafaunal burrowers. Certainly, in the centre of the ground, with additional daily inputs of fine particulate matter, sediments are probably too soft to support large

sedimentary structures. Atkinson et al. (1987) noted in the aquaria that sediment had to be well compacted to support the large and shallow burrows of L. lampretaeformis. To the east and north-east of the centre, sandier patches were observed from previous localized dumping of dredge spoil. These patches were easily identified by the high densities of ophiuroids (Ophiura albida and O. texturata). They generally had lower megafaunal abundance and were also, it seemed, unsuitable for burrowing.

The reduction in megafaunal burrowing species would have the resultant effect of a reduction in large-scale bioturbatory processes. Rhoads & Boyer (1982) and Aller (1982) have reviewed the effects of the marine benthos on the physical and chemical properties of sediments (see also Chapter 1). They noted that important effects were exhibited on nutrient cycling and the general transport of oxygen, water, particles, pore water metabolites, metal sulphides and organic degradation products. From the point of view of megafaunal species, this would lead to heterogeneous sedimentary fabrics, a deep redox discontinuity layer associated with deep sedimentary oxygenation and a degree of topographical relief. The large-scale reduction of these processes in the absence of megafauna has a considerable implication for macrofaunal community structure; as well as disturbance effects, megafaunal species could, by their activity, be considered to be sedimentary conditioners, producing the right environment for a variety of other species.

Macrofaunal successions in response to organic enrichment have been well documented (reviewed by Pearson & Rosenberg, 1978). They have been seen as smooth transitions, normally dependent on the dispersion and organic loading of the system. In certain systems, however, with a well developed burrowing community, the transition may be much sharper than expected at the point where the burrowers are excluded.

5.5.4.2 The Effects on Juvenile Forms

The life-histories of many species are poorly understood and the tolerance of post-larval and juvenile stages even less so. Previous studies of megafaunal burrowing species have been mainly concerned with finding optimum conditions for the culture of economically important species and have been mostly centred around the effect of fluctuating temperature and salinity, Juvenile stages would be more at risk from overburdens and sedimentation and it is thought that they may also be more susceptible to low oxygen tensions and sulphide toxicity. However, this is largely speculative and is perhaps an area that needs greater study. In the case of N. norvegicus, juveniles appear to recruit to the benthos via adult burrows (Smith, 1987).

5.5.4.3 Changes in Interactive Processes

In common with the previous section, this is also an area where little hard information is known. However, if normal individual behaviour rhythms are upset, species may react differently to other factors. In terms of predator/prey relations this could be potentially disastrous. Prey species may be affected, for example, the increased emergence of Scolelepis fuliginosus due to hypoxia (Pearson et al., in press) may make this species more prone to predation. In a similar fashion macrofaunal species may be more susceptible to megafaunal disturbance from, for example, burial.

If, on the other hand, a predator is unable to feed due perhaps to the switch in energy requirements from feeding to respiration, prey species would benefit and the predator may starve. Hagerman & Uglow (1985) discussed some interesting effects on Nephrops norvegicus in relation to food availability. They concluded that this crustacean was well able to meet respiratory stresses from low oxygen tensions provided it could obtain enough suitable food. If the bottom fauna was affected in such a way that less food or food of insufficient quality was available (for example from increased

eutrophication), N. norvegicus may be more susceptible to moderate hypoxia and more readily be induced to leave their burrows. This may occur at Garroch Head since there is a change in fauna towards the centre of the dumping ground. Beyond its burrow it would be more susceptible to predation and fishing pressure. Increased catches have been reported in the Kattegat in relation to low bottom water oxygen content by Bagge & Munch-Petersen (1979) and Rosenberg (1985). Fishing pressure may also be an important factor at the sludge dumping ground, from the observation of fishing boats in the area and trawl marks along the sea-bed.

5.5.4.4 Low Oxygen and Anaerobic Conditions

Since regular annual surveys were first undertaken in 1979, bottom waters over the dump area have remained fully oxygenated during the sampling period, with no sign of hypoxia (Pearson, 1986, 1987). However, samples have not been taken throughout the year and there is a possibility that the oxygen content of the bottom waters is seasonally variable. This has been shown to be the case where the combined processes of water column stratification and eutrophication of surface waters had lead to seasonal deoxygenation of bottom waters and consequent mortality of benthic animals in the Baltic, Kattegat and Skaggerak (reviewed in Rosenberg, 1986). This has also been observed recently in the south eastern North Sea (Westernhagen et al., 1986).

An extremely high BOD/COD would be required to deoxygenate bottom waters over a long enough period to alter benthic community structure. A further requirement would be lack of bottom water mixing and movement. Although residual currents driven by tidal streams over the dumping ground are generally low ($< 10\ cm^{-1}$), additional wind driven flows can cause rapid renewal of the bottom waters (Dooley, 1979). This would prevent all but episodic deoxygenation of the bottom waters over the dumping ground.

Generally, the sediment/water boundary interface would also be oxygenated and a steep gradient of oxygen depletion into the sediment would exist. Jorgensen (1977) pointed out that the steepest gradients are obtained at the surface of completely reduced sediments, where hydrogen sulphide reaches the oxygen of bottom waters. This was characterized in this study by the presence of Beggiatoa spp. (and other related thiobacilli) on the sediment surface of the control area of the dumping ground. Jorgensen reported that these species require both oxygen and sulphide for their metabolism. By the development of dense bacterial mats on the sediment surface, chemical gradients are further steepened by the impedence of microturbulent mixing. He further pointed out that although Beggiatoa spp. were conspicuous by the presence of dense white mats, in the absence of these mats they could still be the most dominant organisms present in sediments. Their presence may therefore be a good indicator of strongly reducing (anaerobic) conditions, but the absence of any white mat does not necessarily indicate the absence of reducing conditions.

Reduced sulphides are potentially toxic compounds and, in addition, Theede et al. (1969) have shown that the presence of hydrogen sulphide in an oxygen poor environment caused increased mortalities in a number of benthic invertebrates.

5.5.4.4.1 Megafaunal Tolerance to Low Oxygen Tensions

The oxygen tension of bottom waters may often be quite high, but within burrows the high surface area to volume ratios will enhance the effect of a specific sedimentary BOD/COD in deoxygenating the burrow water. This would be in addition to the respiratory requirement of the particular burrowing species.

An early review of anoxia tolerance in crustacea by von Brand (1946) led him to conclude that decapod crustaceans showed little tolerance. It has

become evident in more recent studies that anoxia tolerance is an adaptation exhibited by a number of decapods that burrow in potentially hypoxic substrates. In particular this has been demonstrated in the thalassinids Callianassa spp. and Upogebia spp. by Thompson & Pritchard (1969), Felder (1979) and Hill (1981). Because of the environments they inhabit (subtropical intertidal mudflats), burrow water can become hypoxic and often anoxic. These two genera were shown to be adapted to low oxygen tensions by low metabolic rates, metabolic regulation and the ability to survive several days of anoxia (Thompson & Pritchard, 1969). Their results agreed with the hypothesis that metabolic requirement was closely correlated to the availability of oxygen in the environment.

The hypoxic respiratory abilities of burrowing species from British waters has only recently been the subject of study. Table 5.4 shows the critical oxygen tensions (P_cO_2) and burrow water oxygen tensions (P_bO_2) from the lower burrow area of the megafaunal burrowers found in this study, preceeded by the same data for the above-mentioned thalassinids. The critical oxygen tension is defined as the tension below which that species goes into anaerobic metabolism. Values are given in Torr (mm of mercury), saturated seawater having a value in the region of 150-160 Torr.

The sub-tropical thalassinids possessed very low critical oxygen tensions to cope with natural low burrow water tensions. Burrow water tensions were reported to drop on occasion to zero. These species overcame this by anaerobiosis, tolerance to anoxia and the ability of some of the species to come partially out of the water within the burrow to respire aerially (Hill, 1981). The critical oxygen tensions of the burrowing fish (Cepola rubescens and Lumpenus lampretaeformis) were higher than those of the crustaceans, most likely reflected by their ability to swim up into the water-column and away from a particular area. The latter four sub-tidal species had higher burrow water oxygen tensions, probably reflected by their ability to irrigate

Table 5.4 Critical oxygen tensions (P_cO_2) and burrow water oxygen tensions (P_bO_2) of a range of megafaunal burrowing species from the literature.

	P_cO_2	P_bO_2	Authority
Callianassa jamaicense	10-25	0-5	Felder (1979)
C. californiensis	10-20	0-23	Thompson & Pritchard (1969)
Upogebia pugettensis	45-50	14-22	Thompson & Pritchard (1969)
Calocaris macandreae	15	20-40	Atkinson & Taylor (1988)
Nephrops norvegicus	40	80-100	Atkinson & Taylor (1988)
Lumpenus lampretaeformis	50-60	-	Pelster (1985)
L. lampretaeformis	-	57-129	Atkinson et al. (1987)
Cepola rubescens	50-70	60-94	Atkinson et al. (1987)
C. rubescens	-	83	Pullin et al. (1980)

their burrows by continually bringing in new water if necessary (although such activities may be less frequent in C. macandreae.

The critical oxygen tension and burrow water tension of N. norvegicus were both higher than those of C. macandreae which again was probably reflected by the greater mobility and intermittent presence on the sediment surface of N. norvegicus. Other decapod crustaceans have been shown to migrate in response to fluctuating anoxia (Burd & Brinkhurst, 1985). C. macandreae has not been observed leaving established burrow systems, except following catastrophic disturbance, for example, the incursion of resin into the burrow from resin casting. It has been shown to survive at least 20 hours total anoxia, but even then did not leave its burrow (pers. comm., S. Anderson). Because the burrow of C. macandreae has much smaller diameter, the relatively higher surface to volume ratio would have a considerable implication. A fixed BOD/COD would have a much greater impact than in the burrow of N. norvegicus. The low critical oxygen tension of C. macandreae must therefore be an adaptation to a life in conditions of depressed oxygen tension.

An emergence response to hypoxia has been demonstrated for N. norvegicus by Hagerman & Uglow (1985). However, individuals were shown to become tolerant to low hypoxia levels and would remain in their burrows. As discussed in Section 5.5.5.4.3, this was suggested to be dependent on food availability. On this point, Hagerman & Baden (in press) have recently suggested that hypoxia affected the foraging activity of N. norvegicus and that resultant starvation induced low haemocyanin values, which lessened the tolerance to further hypoxia.

The presence of a number of large individuals of N. norvegicus on the sediment surface during the video survey in daylight hours could not conclusively be put down to hypoxic conditions within their burrows. Small individuals were not observed at all during the survey. Burd & Brinkhurst

(1985) investigated the effect of oxygen depletion on the squat lobster Munida quadrispina. They suggested that larger individuals were better adapted to low oxygen tensions. They observed that only the largest individuals tolerated hypoxic conditions (down to approximately 3 Torr); these individuals exhibited the lowest critical oxygen tensions and in comparison to smaller sized individuals possessed relatively larger gills.

No data are available on the respiratory physiology or adaptions of Callianassa subterranea. It is thought that because of its deep burrowing mode with restricted surface access (Atkinson & Nash, 1985; this study), this species would have a low critical oxygen tension and in common with the sub-tropical thalassinidians be somewhat tolerant to anoxia. Another thalassinid, Axius serratus has been reported to burrow deeply (3 m) in polluted sediments (Pemberton et al., 1976) and must be well adapted to tolerate low oxygen tensions and anoxia.

The range of critical oxygen tension values for Lumpenus lampretaeformis was slightly lower than that of Cepola rubescens which reflected no doubt the more confined nature of the burrow of the former. Both can probably tolerate low level hypoxia and by burrow irrigation, can probably prevent levels from dropping too low. It is interesting to note that Pelster (1985) also gave a critical oxygen tension for the intertidal goby Blennius pholas of 20-30 Torr, a very low value. This goby inhabits the intertidal zone and retreats under rocks and stones at low tide and is often in anoxic conditions with fluctuating high temperatures.

The oxygen tension figures from the literature were all obtained from experimental aquaria or from relatively 'normal' burrowed areas, on adult specimens. Most of these species can tolerate low level hypoxia. Unfortunately, little information is available on their behavioural responses to hypoxia, except for the emergence of N. norvegicus mentioned above. If low oxygen tension was the primary controlling factor of adult megafaunal

abundance at the sludge dumping ground, C. macandreae would be expected to extend furthest in towards the centre. In a similar fashion, the active burrowing fish L. lampretaeformis would not be expected to extend as far. However, neither of these hypotheses was borne out, indicating that oxygen depletion is not the primary controlling factor, but may still be an important determinant in conjunction with other factors.

5.5.5 Conclusions

The dumping of sewage sludge at the Garroch Head ground undoubtedly has an inhibitory effect on megafaunal organisms. Deposition of sludge is the main cause, but the effects are thought to be due to a complex of factors which involves principally, sedimentary modifications, the effects on juvenile stages and anaerobic conditions. The response of individuals and species may initially vary, but it results in the absence of megafaunal burrowers in the middle of the ground.

Where the megafaunal burrowers are reduced by increased sludge effects, there will be a more severe implication for the macrofaunal community. On the positive side an agent of disturbance is removed, but on the negative side, a large-scale bioturbatory agent is removed. Deep aeration, sediment turnover and solute transport would be considerably reduced. Added to the increased sludge loading nearer the centre of the ground, the sediment would become more quickly anoxic leading perhaps to a more abrupt change along the enrichment gradient than has previously been suggested.

CHAPTER 6. GENERAL DISCUSSION

6.1 The Determination of Community Structure

Many, often conflicting theories, have been proposed to explain the observed structure of marine benthic communities. Recently, Pearson & Rosenberg (1987) have clarified an approach hinted at by a number of authors (recently Smetacek, 1985), integrating some of the established ideas into a hierarchical scheme based upon food availability as the primary constraining factor. Hierarchical schemes which involve the use of multiple limiting factors, are not new and have previously been suggested by Wildish (1977), Erwin (1983) and Zajac & Whitlach (1985).

Pearson & Rosenberg (1987) described a number of modifying factors which they felt influenced food availability, which included as primary factors, latitude and depth and as a secondary factor water movement. Physical factors, stochastic events and biotic interactions were also noted as both dependent and independent modifying factors that further influenced species distributions. These interacting environmental factors were placed by the authors into a hierarchical scale of impact, affecting different levels of community structure. They conjectured that "the megastructure, i.e. the distribution of major functional groups within the community is determined by the effect on food availability of changing depth, latitude and current speed. The macrostructure, principally the divisions within functional groups which define successional phenomena and selection of life history characteristics, is determined primarily by the general modifying factors which define the degree of environmental harshness. Independent modifying factors, principally biotic interactions, define the microstructure of the community, i.e. the small scale patchiness and degree of local variability."

The communities investigated in the course of this study were all similar in terms of megastructure. Food availability and localized water movement may have played an important role in their original environmental determination, which has resulted in broadly similar structures at this scale. Some differences were evident at the macrostructural level. Although factors such as temperature, salinity and dissolved oxygen would be similar, organic carbon content, sediment type, relative depth and other localized characteristics including some stochastic events (alginate waste input and fishing pressure) were shown to cause intrinsic differences. This was demonstrated, for example, by the very high abundance of surface deposit feeding species at the Loch Creran site, thought to be due to localized organic enrichment.

As Pearson & Rosenberg (1987) pointed out, biotic interactions may be the major source of small scale patchiness (microstructure) in the community. Several biotic factors are now understood to cause patchiness and some have been considered to be primary structuring forces in community determination. These factors include, for example, predation, competition, disturbance, adult-larval interactions, trophic group amensalism and the mobility mode hypothesis. They show a high degree of complexity and some inter-relation.

Megafaunal burrowing activity is an important factor in the widespread formation of small scale heterogeneous patches. This was visibly evident and was demonstrated in terms of spatial variation at the community and species level and in physico-chemical properties, both by random large scale area sampling and by fine scale sampling of burrowed and non-burrowed areas.

The influence of megafaunal activity in determining community structure has been divided into a number of specific processes in Table 6.1, which also highlights the principal faunal groups affected. These data, which summarize the work of this thesis, are illustrated schematically with overlapping interactions in Figure 6.1. Megafaunal effects are shown

Table 6.1 The effects and consequences of megafaunal activity on sedimentary processes.

Process/Factor	Changes Induced by Megafaunal Activity	Consequences for Principal Faunal Groups	
		Primary - Direct Effects	Secondary - Indirect Effects
INHIBITION			
Interference	(Direct)	Generally reduced macrofaunal activity especially in near-surface dwelling sessile fauna	Reduction in microbially mediated chemical processes.
Predation	(Direct)	Reductions in numbers of macrofauna, especially near-surface dwelling species	Reduction in microbially mediated chemical processes. If macrofaunal predators are the preferred party, reduced macrofaunal predation would result.
Particle mixing	Increased	Reduction in numbers of sessile and suspension feeding species	Possible reduction in macrofaunal bioturbation. Enriched sediment if affected groups die off and decompose.
Resuspension	Increased	Clogging of suspension feeders, small individuals and juveniles washed out	Possible reduction in macrofaunal bioturbation. Enriched sediment if affected groups die off and decompose.
Sedimentation	Increased	Burial of sessile, surface feeding and juvenile organisms	Possible reduction in macrofaunal bioturbation. Enriched sediment if affected groups die off and decompose.
Median grain size of surface sediments	Decreased	Reduced chance of adult replacement by grain-size dependent juveniles	-
Compaction	Increased	Increased difficulty burrowing and reduced aerobic microbial activity	If macrofaunal predators are affected, reduced predation. Reduced food for deposit feeders.
Microbially mediated chemical processes	Decreased	-	Reduced processes from reduced macrofaunal bioturbation. Provides less food for deposit-feeders.

Table 6.1 (continued)

Process/Factor	Changes Induced by Megafaunal Activity	Consequences for Principal Faunal Groups	
		Primary - Direct Effects	Secondary - Indirect Effects
ENHANCEMENT			
Particle mixing	Increased	Increased activity of burrowing deposit feeders	Enhanced macrofaunal bioturbation, increased aerobic microbial activity
Resuspension	Increased	Increased feeding material for suspension feeders (until threshold is reached, then inhibitive).	Increased biodeposition in form of faecal pellets.
Sedimentation	Increased	Increased feeding material for surface deposit feeders.	Increased biodeposition in form of faecal pellets.
Median grain size of surface sediments	Increased	Attraction for species with larvae possessing particular grain size requirements.	-
Compaction	Increased	Increased anaerobic microbial activity	Enhanced feeding for deposit feeders.
Surface Area	Increased	Increased area for aerobic microbial activity. Increased space for surface deposit feeders.	Enhanced feeding for deposit feeders.
Detrital food Resources	Increased	Increased food for deposit feeders and scavengers from burial of introduced organic material. Deep particles uncovered and decomposition of dead organisms.	Increased prey for macrofaunal predators, increased bioturbation.
Microbially mediated Chemical Processes	Increased	Enhanced aerobic microbial activity	Enhanced feeding for deposit feeders.
Oxygenation	Increased	Increased living space for macrofaunal burrowers, aerobic microbes.	Increased prey abundance and food availability for deposit feeders.

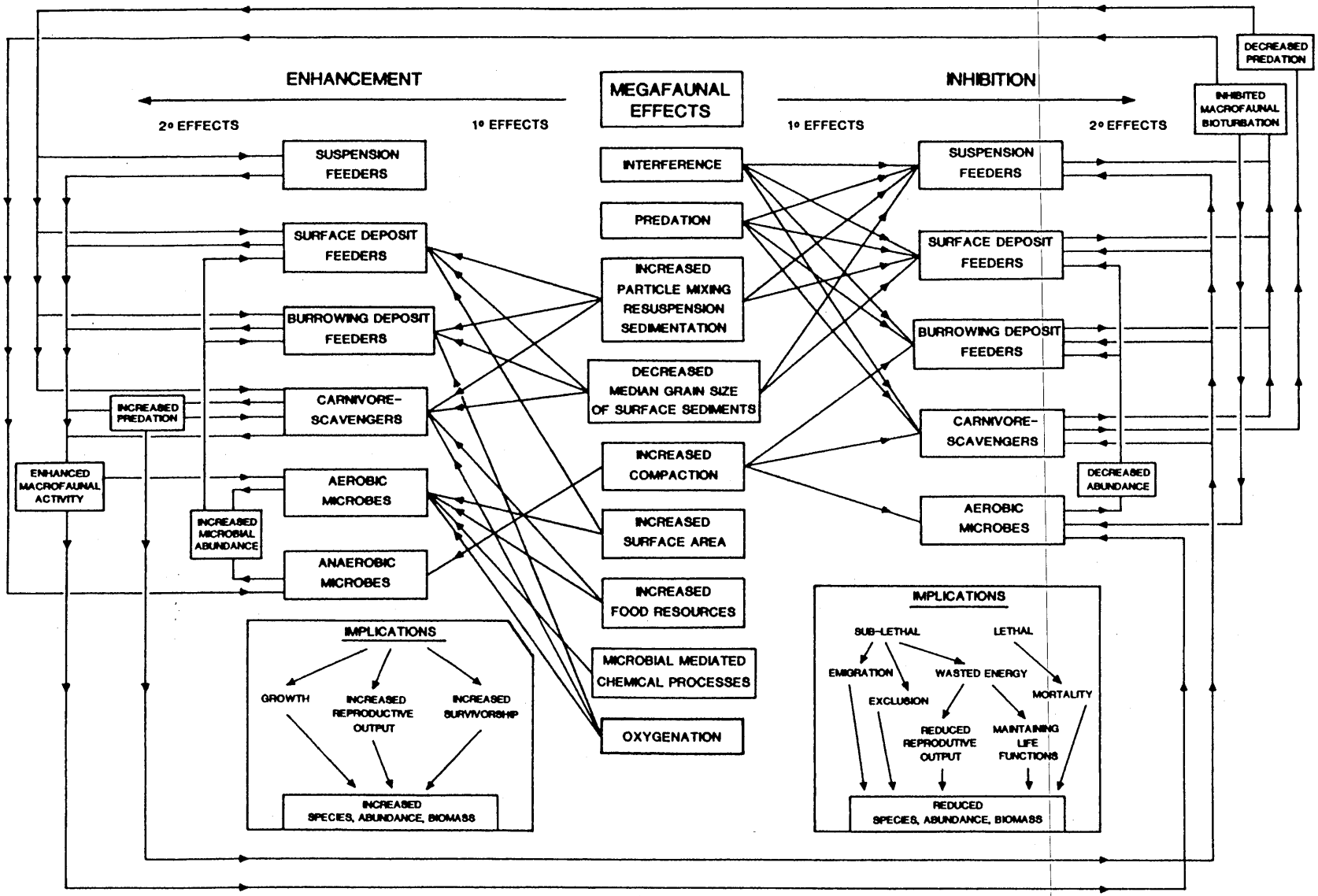


Figure 6.1 The inter-relationship of different megafaunal effects on the sedimentary environment and principal faunal groups, with the implications for community structure.

vertically in the centre of the illustration, with direct inhibition and enhancement effects radiating off. Secondary effects mediated through biotic interactions (inhibitory and enhancing) are shown towards the outer edges of the illustration. Many of the established theories of the influence of biotic interactions mentioned above are represented in these effects, including components of predation, competition (including amensalistic interactions) and disturbance. This further emphasizes the complexity and inter-relation of such interactions. Below I summarize these established theories and show how the effects of megafaunal burrowing activity relate to them.

6.1.1. Competition

Competition in soft sediments has been reviewed by Woodin (1983) and Branch (1984). It may exist either in the form of direct or indirect interactions. Direct competition involves actual contact between organisms or direct interference in life functions (Woodin, 1983). This could take the form of aggression responses, for example, between spionids (Levin, 1982); it could be interspecific or intraspecific and may result in either exclusion by emigration or mortality, or co-existence with probable reduced growth. In terms of competition for space, megafaunal burrowers directly interfere in the normal lifestyle of many macrofaunal species. This was observed on surface visible fauna, but could only be assumed for burrowing species, on the supposition that deep megafaunal excavations, at the very least, exclude deep burrowing macrofaunal species from the actual space occupied by the burrow.

Evidence of interspecific competition in soft sediments is very limited (Dayton, 1984). Dayton noted that in most infaunal systems, there were no data supporting strong competition for a potentially limiting resource. In a recent review, Peterson (1979) argued that most sedimentary infaunal communities can have very large increases in densities (as a result of predator exclusion) without any evidence of competitive exclusion. This echoed earlier

comments by Connel (1975), who observed that many species seldom reached population densities great enough to compete for resources, because either physical extremes or predation eliminated or suppressed them in their young stages. Whitlach (1980), in one of the few studies on infaunal competition within functional groups, pointed out that differences in vertical space utilization were apparently an effective mechanism for reducing interspecific competition, but "diffuse competition" may be more important than previously realized in the organization of infaunal communities. Diffuse competition was previously defined by Diamond (1975), as a type of interspecific competition resulting from the combined effects of several closely related species, which results in the competitive exclusion within species groups, guilds or functional groups.

Indirect competition does not involve interference and may be divided into two levels: within a functional group (for example a feeding or mobility group, which may include several different taxa), or between different functional groups. Within a functional group, indirect competition may take the form of resource pre-emption, where one or more (diffuse competition) species may be more efficient at utilizing a resource. Indirect competition at the functional group level may be mediated through density-dependent modification of the sediment (on some occasions this may be caused by one especially dominant or abundant organism). The activity of one group may make the substratum less suitable for another group. This has been documented in terms of feeding groups by Rhoads & Young (1970) in the Trophic Group Amensalism theory and in terms of motility groups by Brenchley (1981) in the Mobility Mode Hypothesis. Both these theories can be termed "functional group amensalisms". Rhoads & Young (1970) suggested that deposit feeders exclude suspension feeders from soft sediments by their activity, in that they produce a fluid-like faecal rich, easily resuspended sediment. This clogs the suspension feeders, buries or resuspends newly

settled larvae or discourages initial settlement and prevents attachment by sessile epifauna. This theory was also supported by the work of Bloom et al. (1972), Aller & Dodge (1974), Myers (1977b) and others. (The mechanisms of most amensalistic interactions are concerned with sedimentary disruption and are included in the following section.)

The ideas of Brenchley (1981, 1982) ran along very similar lines. Her experiments, however, led her to believe that in bioturbated areas, the sessile species (effectively suspension feeders, but also including tubiculous deposit feeders) were more at risk and declined in abundance to the benefit of more mobile species. This work has been supported by the studies of Murphy (1985) and Posey (1986), amongst others. In a recent review, Posey (1987) re-evaluated the conditions necessary for mobility related interactions to regulate community structure and suggested that they may only become important in those specific instances when dense species assemblages containing large or active organisms are involved. Both theories have been proven, and the exact type of amensalism which occurs depends on the combination of species present.

Perhaps the greatest impact due to megafaunal activity was that described by functional group amensalism. Some of the individual burrowers (Nephrops norvecigus, for example), were of such a large size and impact that they were responsible for a non-density dependent amensalism around their burrows and associated area (in contrast to the density dependent modifications discussed above). The general activity of megafaunal burrowers had the overall effect of excluding a number of surface dwelling, discretely motile or sessile tubiculous species, such as spionids and maldanids from the vicinity of burrows. These species were found to be more abundant in areas away from burrows, areas that may act as refuges. Both field and experimental results were indicative of a mobility mode amensalism.

6.1.2. Disturbance

Density dependent modification of the sediment constitutes a type of sediment mediated biological disturbance. Thayer (1983) and Probert (1984) have reviewed these types of disturbances and their importance in determining community structure. Probert (1984) stressed the increasing importance of biologically induced modifications to the sediment water interface, when physical processes become less rigorous or infrequent. This would particularly apply in soft muddy sediments. Thayer (1983) characterized seven basic modes of disturbance or amensalism between mobile bioturbators and sessile or relatively immobile organisms. These included: bulldozing (displacement and manipulated), ingestion/egestion(whilst mining), pseudofaeces from deposit feeders, biodeposition (from pseudofaeces and defaecation), biotic resuspension, fluidizing and finally destabilizing (facilitating physical erosion and resuspension). Thayer suggested the following strategies for "winning the war of sediments": 1) be large; 2) be mobile and/or disturb the sediment rapidly; and 3) occur in dense populations.

Megafaunal bioturbatory activity is associated with most of Thayer's modes of disturbance. Although N. norvegicus is not a deposit feeder, the thalassinid infraorder (including Calocaris macandreae and Callianassa subterranea) is thought to be comprised mainly of sediment ingestors and they will thus cycle and modify sediments through their guts. In doing so, they may alter the rate of sedimentary microbial processes, secondarily affecting macrofaunal deposit feeders. Bulldozing, however, has perhaps the greatest impact especially in terms of adverse consequences, for relatively immobile organisms. Buried or inverted epifauna and surface dwelling species are likely to die unless they can re-establish contact with the water column for feeding and respiration. Animals that can regain functional orientation, waste energy in the process (Myers, 1977b). Exhumed infauna may be eaten (Myers, 1977b; VanBlaricom, 1982) or be swept away. Newly settled juveniles would be

especially susceptible (Rhoads & Young, 1970; Woodin, 1976). This vulnerability may be increased in seasonal climates, for larval settlement and peak disturbance rates are both likely to occur when waters are warm (Thayer, 1983).

Trampling and compaction could be added to Thayer's modes of disturbance. The possibility of their occurrence was evidenced by the reduction in macrofauna in the entrance to the burrow of N. norvegicus and in the formation of an RPD layer, in response to the activity of that species, in the experimental mesocosms in Chapter 4.

Megafaunal bioturbatory effects were observed to be differential and were related to the particular life-style and general activity of each species. N. norvegicus, a large surface active bulldozer, had a much greater inhibitive effect than the more inactive burrower Calocaris macandreae.

6.1.3. Predation

The importance of predation in structuring sedimentary communities has recently been stressed by many authors (Peterson, 1979; Summerson & Peterson, 1984; Commito & Ambrose, 1985a; Reise, 1985b; Ambrose, 1986; Wilson, 1986). Sedimentary environments are three dimensional and unless a predator can follow its potential prey into the sediment, sub-surface levels will serve as an effective refuge. Woodin (1983) subdivided predators into a number of type categories. Species which predate at the sediment surface may be either epifaunal or infaunal and may include many species of fish, crabs and shore birds in the intertidal zone, as well as a diverse number of infaunal organisms. They range from the sediment disturbers mentioned above, to browsers nipping siphons, tentacles and palps. As well as carnivores, a number of surface deposit feeders, suspension feeders and omnivore/scavengers are known to ingest juveniles. This is a very important aspect of predation and is normally referred to as adult-larval interactions

(Woodin, 1976), but it may also include interactions with invading juveniles and adults. A suite of species can prevent further invasion by juvenile/larval ingestion and may thus avoid subsequent increased interspecific and intraspecific competition (Bonsdorff et al., 1986).

A number of authors have observed that the activity of predators can also constitute a major disturbance, particularly when they are large, epifaunal or demersal-feeding (Woodin, 1981; VanBlaricom, 1982; Oliver et al., 1984; and others). In the process of pit digging for preferred prey, rays may expose and flush out other infaunal species that are immediately consumed by other fish (VanBlaricom, 1982). The effects of epibenthic predation may be differential affecting mostly sessile surface dwelling species. The ability to survive would be enhanced by the presence of a thick tube, mobility, the ability to retract quickly or a deep dwelling life-style.

Reise (1985b) pointed out that epibenthic predation often severely reduced the infauna, maintaining it far below carrying capacity. This predation was intermittent, although balanced somewhat by the intense interactions between predators. It was lessened by prey refuges and predator avoidance mechanisms and was occasionally interrupted by large scale physical disturbances. He found that these latter events gave rise to a few opportunities for competitive interactions, primarily intraspecific.

In contrast to surface predators, Woodin (1983) also categorized 'weasel' digging and burrowing predators. Weasel analogues were described as predators that followed an organism down its siphon hole or burrow opening. Digging predators excavated their own hole down to a prey item and burrowing predators moved within the sediment hunting prey, for example, some glycerid polychaetes (Okelmann & Vahl, 1970).

Predatory interactions are structurally complex and can exist at a number of different hierarchical levels, including both infaunal and epifaunal species (Reise, 1985a, 1985b; Commito & Ambrose, 1985a, 1985b). Reise

(1985b) suggested that the activity of resident endobenthic predators (lower down in the hierarchy) was continuous and discrete in contrast to the more seasonal and episodic epibenthic predation.

The predatory diet of N. norvegicus is well documented (see Section 3.4.2.) and some evidence of predation has been presented for C. macandreae (Perez, 1981), although the exact nature of the diet of this latter species is still not fully understood. The impact of predation by megafaunal burrowers on macrofaunal community structure is also little understood. The situation is further complicated by secondary effects, caused by the bioturbatory activities of these species. If macrofaunal predator/prey relationships are unbalanced, megafaunal species may indirectly cause increases or decreases in macrofaunal predation.

6.1.4. Macrofaunal Enhancement

Megafaunal activities are not wholly inhibitive and aspects of biological enhancement were observed. Their importance in aeration, solute transport, nutrient cycling and general sediment conditioning are stressed in Section 5.5.4.1. The increase in surface area due to the presence of megafaunal burrows has not only a considerable implication in increasing the rate of these processes, but also in stimulating microbial growth (Driscoll, 1975; Yingst & Rhoads, 1980).

Some species seemed to respond to a resource provided directly or indirectly by the burrowers (organic rich sediment and enhanced microbial activity). In the case of N. norvegicus, the number of nematodes and oligochaetes increased in the vicinity of its bulldozed area, whilst Corbula gibba and Turritella communis increased in density around the excavated sediments of C. macandreae, presumably an organic rich area. High meiofaunal and microfaunal abundances have been shown by Reise (1981a, 1981b, 1985a) to be associated with biogenic structures. Warwick et al.

(1986) reported an increase in meiofaunal abundance on a large polychaete faecal mound, in contrast to Thistle (1980), who reported a less dense assemblage of harpacticoid copepods on the faecal mound of an enteropneust. In particular, McIntyre (1973) has recorded a high abundance of meiofaunal species at the entrance to a burrow of N. norvegicus. He suggested that this area may act as a refuse dump or larder, providing a rich bacterial feeding ground. In response to colonization by a megafaunal burrower (an enteropneust), Flint & Kalke (1986) observed a shift in macrofaunal community structure and a general increase in abundance. This was due to the further colonization by early successional type species and was associated with increasing depth of the aerobic layer and an increase in sedimentary organic content.

Thistle (1981) suggested that early colonizers of disturbed areas do not respond to the lack of competition in a defaunated area, as was previously thought by many authors, but respond to the provision of a new or unexploited food resource. Relict burrows have been shown by Aller & Aller (1986) to act as traps for active organic matter and were sites of enhanced biological activity. In a continuously disturbed area, however, persisting animals must show a high degree of tolerance or adaptation and non-tolerant species would be excluded.

6.2 Spatial and Temporal Heterogeneity

After a particular disturbance event an area of sediment may be defaunated. Following a natural successional sequence after recolonization, the community may show multiple stable points and possess neighbourhood stability, so corresponding to the terrestrial ecologists' poly-climax theory of community development (Gray, 1977, 1981). Gray noted that the early successional stages were reasonably predictable, but as the succession continued it became increasingly variable and could end at any one of a

number of stable points each dominated by different species, all dependent on the influence of local historical events. The existence of multiple stable points has, however, been recently criticized by Connel & Sousa (1983). They argued that the minimum time period for which an assemblage may be judged as stable was over one complete turnover of the adult species concerned. This, they noted, has rarely been demonstrated. Connel & Sousa found the concept of persistence (within stochastically defined bounds), rather than stability, to be more applicable in real ecological systems.

The primary determinants of an estuarine succession suggested by Zajac & Whitlach (1982) included: timing of disturbance, habitat of disturbance, reproductive periodicity of the infauna, ambient population dynamics and abiotic and biotic factors.

Within megafaunal burrowed patches, macrofaunal community structure was found to be significantly reduced. Recolonization of these patches may therefore have been expected, by either larval settlement or adult immigration. No typical primary colonizing opportunist species were recorded, for example, Capitella capitata and Scolelepis fuliginosus (Pearson & Rosenberg, 1978), which were present in areas adjacent to those investigated in this present study. McCall (1977) demonstrated that equilibrium species (the opposite of opportunistic, in that they are generally large, mobile, exhibit slow development, few reproductions per year, low recruitment, low mortality rate) could also settle with early colonists, remaining at low but constant abundance. However, larvae may avoid settlement in these areas due to the continuous nature of the disturbance and general sediment instability. Wilson (1952) noted early on that macrofaunal larvae could delay metamorphosis until a suitable substratum was contacted and Gray (1971) further observed that substratum selection was better developed in the larvae of sedentary adults, probably due to their high stability requirement. Away from mechanically disturbed patches, larvae may settle but would have to contend with the

increased factors of macrofaunal predation, competition, and adult-larval interactions, all of which may be more limiting for opportunistic species.

A number of early successional species (Pearson & Rosenberg, 1978) were present at some of the burrowed study sites (for example, Prionospio malmgreni, Scoloplos armiger, Corbula gibba and Thyasira flexuosa). However, it was felt that these species were responding to a generally enhanced sedimentary organic content and none were observed in the close vicinity of actively burrowed areas.

Any recolonization of the burrowed areas was most likely to be from adult immigration, the probability of which is inversely related to the size of the area (Probert, 1984). Small areas are more liable to adult recolonization, a process that may be reasonably rapid (Bell & Devlin, 1983), depending on the relative mobility of these adult organisms. They may of course be the same individuals that emigrated away from the original disturbance. Not all species may be removed by a disturbance and these residual species may significantly influence the recolonization process, depending on their activity (Woodin, 1976).

The size and scale of disturbed patches depends much on the type and extent of disturbance, which in turn is dependent on the particular burrowing species. C. macandreae may disturb a small surface area around its burrow openings, extending to a depth of approximately 15-20 cm around its gallery system. The callianassid-type burrows would probably only affect the area immediately surrounding their main volcano-like openings and a small downstream area influenced by the deposition of resuspended sediments. Their gallery system would be beneath the inhabited area of most infaunal species (10 cm - cited by Holme, 1964), but a number of larger species which may extend to levels deeper than 40 cm (Keegan & Konnecker, 1973) may be affected. The area affected by N. norvegicus may be much larger (even without the inclusion of its foraging area), with an extensive bulldozed surface

area, and a gallery system which extends to approximately 20-25 cm depth. The primary patches affected by megafaunal burrowers would be single burrows, which may encompass areas up to a size of several hundred square centimetres. However, burrows may occur in clumps, which act as larger, secondary scale patches over an area of several tens of square metres, resulting in patches within patches.

The efficiency of remote benthic sampling would be lessened in an area where megafaunal burrowers were present, especially if the area sampled is near to the size of the disturbed patches. More samples would be required to lessen the variation in the data obtained to get an adequate understanding of community structure.

As well as a spatially variable component causing local heterogeneity within the community, a temporal component would also exist. Burrowed patches in soft sediments will continually evolve over time as patches grow and decay. There are a number of different time scales involved with megafaunal disturbance, which result in different time scales for temporal heterogeneity. A burrow section may become relict with time and collapse as the occupant moves on to work a new area. This may occur over a period of a few days or months, Yingst & Rhoads (1978) suggested that temperature-related changes in the activity of bioturbators may have caused seasonal differences in sediment stabilty. Myers (1977a) related increased seasonal stability to more effective microbial sediment binding. Naturally occurring periods of increased sediment stability could then be exploited by species normally excluded, for example, discretely motile or tubiculous species, an example of a temporal refuge as described by Woodin (1978). Probert (1984) indicated that seasonal changes may also result from migratory behaviour or changes in foraging activity of bottom feeding predators. Seasonal migration has been suggested in some megafaunal burrowers, for example, N. norvegicus (Andersen, 1962) and Lumpenus lampretaeformis (see Gordon & Duncan, 1979;

Nash, 1980), but these ideas were probably misinterpretations of quiescent periods by those species in their burrows, which resulted in their relative unavailability to fishing activity. Changes in seasonal foraging activity have been observed in N. norvegicus. Chapman (1980) reviewed the ecology of this species and pointed out that cold winter temperatures decreased foraging, whilst low bottom water oxygen levels associated with late summer months in some areas forced many animals out from their burrows. Ovigerous females (in winter months) and newly moulted individuals were noted to be less active.

Further long term time scales may be involved, affecting the temporal stability of a community, mediated through general changes in the megastructure and macrostructure of that community (Pearson & Rosenberg, 1987 - see above). If the physical environment has changed or is changing, megafaunal population structure or behaviour may be affected, and changes would be passed on to macrofaunal community structure, through megafaunal activity. Change in the physical environment may go unnoticed if the time scale involved is over more than a decade, as only very few repeat benthic studies are longer than this.

In conclusion, the continuous but haphazard activity of megafaunal burrowing species, which involves many inter-related processes, is an important factor, previously overlooked in maintaining patches at different states of dominance, thus increasing the spatio-temporal heterogeneity in temperate marine soft sedimentary communities.

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Appendix 1

Taxonomic Keys for the Identification of Species Found

Anthozoa		Manuel (1981)
Polychaeta	General:	Day (1967)
		Fauchald (1977)
		Fauvel (1923, 1927)
		Banse & Hobson (1974)
		Hobson & Banse (1981)
	Nephtyidae	Rainer (1984)
	Spionidae	Blake & Kudenov (1979)
	Paraonidae	Hartley (1981)
	Capitellidae	Hartman (1947)
	Ampharetidae	Day (1964)
	Terebellidae	Pearson (1969)
		Holthe (1975)
Sipunculida		Gibbs (1977)
Mollusca	Prosobranchia	Graham (1971)
	Opistobranchia	Thompson & Brown (1976)
	Lamellibranchia	Tebble (1966)
Echinodermata		Mortensen (1927)